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Reports
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COOP AGREEMENT
UNIV OF MONTANA

FINAL REPORT FOR RESEARCH AGREEMENT
#INT-95086-RJVA
"Replacement of Whitebark Pine by Subalpine Fir: The Consequences for Stand Carbon, Water and Nitrogen Cycles"
UNIVERSITY OF MONTANA
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Replacement of whitebark pine by subalpine fir: the consequences for stand carbon, water and nitrogen cycles.

Report to the USDA Forest Service, Intermountain Research Station,
Intermountain Fire Science Laboratory

Joint Venture Agreement INT-95086-RJVA
August 1995- September 1998

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September 1998

Succession may maintain high leaf area:sapwood ratios and productivity in old subalpine forests.

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Running Head: succession, biomass allocation, and forest productivity

Key Words

allometry, biomass allocation, carbon cycle, climate change, forest productivity, growth efficiency, leaf area, productivity, sapwood, succession

Key Phrases

- succession and changes in forest biomass allocation
- late-successional species and forest sapwood:leaf ratios
- late successional species and the balance of assimilation and respiration in forests
- biomass allocation and productivity in subalpine forests
- forest productivity and age

Abstract

Old forests are generally thought to exhibit low productivity and therefore to be insignificant carbon sinks. This generalization is based, in part, on the hypothesis that the biomass of respiratory tissues such as sapwood increases with age to a point where all photosynthate is required just to maintain existing tissue. However, this theoretical connection between respiration:assimilation ratios and forest productivity is based on age-dependent trends in sapwood:leaf ratios of individual species and even-aged stands, and does not take into account processes in natural forests such as disproportional increases in shade-tolerant species over time and multiple-age cohorts. Ignoring succession and structural complexity may lead to large underestimates of the productivity of old forests and inaccurate estimates of the ages at which forest productivity declines. We compared biomass allocation and productivity between whitebark pine, a shade-intolerant, early-successional tree species and subalpine fir, a shade-tolerant, late-successional species, by harvesting 14 whitebark pine and 9 subalpine fir that varied widely in dbh, and calculating regression models for dbh versus annual productivity, growth efficiency, and biomass allocation to leaves, sapwood, and heartwood. Late-successional subalpine fir allocated almost twice as much biomass to leaves as early-successional whitebark pine. Subalpine firs also had much lower allocation to sapwood and higher growth rates and efficiencies across all tree sizes. We then modeled biomass allocation and productivity for 12 natural stands in western Montana that were dominated by subalpine fir and whitebark pine, that varied from 67 to 458 years in age, by applying the regressions to all trees in each stand. Whole-stand sapwood:leaf ratios and stand productivity increased asymptotically with age. Sapwood:leaf ratios and productivity of whitebark pine in these stands increased for approximately 200-300 years and then slowly

decreased over the next 200 years. In contrast, sapwood:leaf ratios of all sizes of subalpine fir were lower than those of pine, and productivity was higher. As stands shifted in dominance from pine to fir with age, subalpine fir appeared to maintain gradually increasing rates of whole-forest productivity until stands were approximately 400 years old. These results suggest that forests such as these may continue to sequester carbon for centuries. If shade-tolerant species that predominate late in succession maintain high assimilation to respiration ratios in other forests, we may be underestimating production in old forests and current models may underestimate the importance of mature forests as carbon sinks for atmospheric CO_2 in the global carbon cycle.

Introduction

As conifer forests age, net productivity increases rapidly during early successional stages and is thought to decrease to very low or even negative rates in older forests (Bazzaz 1979, O'Neill and DeAngelis 1981, Pearson et al. 1984, Ryan 1991, Ryan and Waring 1992, Gower et al. 1994, Murty et al 1996, Ryan et al. 1997). A widely cited hypothesis for this decline in productivity is that biomass allocation to leaves decreases or reaches a steady state, while allocation to sapwood increases, creating conditions where total respiration costs equal or even exceed gross photosynthetic assimilation (Yoda et al. 1965, Odum 1969, Kira and Shidei 1967, Whittaker 1975, Waring and Schlesinger 1985, Kimmins 1997). Despite the lack of rigorous tests (see Gower et al. 1995), the presence of alternative hypotheses (Vitousek and Reiners 1975, Van Cleve et al. 1981, Gholz et al. 1985, Ryan and Waring 1992, Yoder et al. 1994, Gower et al. 1996, Murty et al. 1996, Ryan and Yoder 1997, Ryan et al. 1997), and evidence that indicates biomass may continue to accumulate for hundreds or possibly thousands of years in some forests (MacMahon 1980, Franklin et al. 1981, Kimmins 1997, Tappeiner et al. 1997), the biomass allocation-productivity paradigm is still central to forest ecology and affects estimation of global carbon budgets. For example, increasing respiration:assimilation ratios are implicit as the mechanistic background for the management practice of replacing old "over-mature" or "decadent" forests with younger even-aged stands to increase forest productivity (Smith et al. 1997*a*). The respiration:assimilation hypothesis is also the theoretical basis for the assumption that old forests play a minor role as an active carbon sink in global models (Detwiler and Hall 1988, Jarvis 1989, Dixon et al. 1994, Mellilo et al. 1995).

A weakness in the current conceptual relationship between forest age, sapwood:leaf allocation, and productivity, however, is that models for sapwood:leaf ratios in whole forests, as they age, have been extrapolated from age-dependent allocational patterns of single species (Turner and Long 1977, Attiwill 1979), even-aged stands (Braastad 1975, Long and Smith 1992, Ryan and Waring 1992, Ryan et al. 1997), combination of many species into a single ratio (Kira and Shidei 1967), or as in Odum's (1969) influential treatise, on generalized theoretical connections between algal microcosms and Kira and Shidei's results. Although increasing sapwood:leaf mass ratios with age are the rule for individual trees, and must eventually occur in undisturbed forests, successional shifts in community species composition and multi-age cohorts (see Haight and Monserud 1990, O'Hara 1996) that typify many natural forests may maintain low sapwood:leaf ratios and high forest productivity for much longer than predicted by allocational changes in single species or even aged stands.

Interspecific comparisons of leaf:sapwood (cross-sectional area at base of live crown) ratios for conifer species in the literature show a correlation between leaf:sapwood proportions and site aridity (Waring and Schlesinger 1985, Margolis et al. 1995, Kimmins 1997). This suggests that the xeric conditions that occur in some early successional sequences (Geiger et al. 1995) may favor species that have relatively low leaf to sapwood ratios (i.e. low transpiration area and high water storage volume). As forests age, low-light conditions may favor species with high leaf to sapwood ratios, an assumption that is generally supported by pairwise comparisons of species that are thought to form general successional sequences in western coniferous forests (Table 1). The observation that leaf areas and leaf:sapwood ratios of late seral species are typically higher than those of early successional species supports the hypothesis that successional processes may maintain a favorable balance of assimilation and

respiration and productivity in older forests. Long-term recruitment after stand initiation may amplify the species-specific effects of late seral species on respiration:assimilation ratios. However, little information exists on biomass allocation of early and late seral species growing under the same climatic conditions at the same site. Most of the ratios presented in Table 1 were collected at different study areas, or over a wide range of biophysical conditions within study areas, and only provide inference for trends that might occur during succession in conifer forests. Compounding our lack of knowledge of the effects of succession on biomass allocation and productivity is the scarcity of field studies that compare productivity among forests of different ages but in similar habitats.

Fire exclusion policies have led to large-scale successional changes in conifer forests throughout North America (Arno 1980) where early seral, single-strata forests have been replaced by late successional species (Covington and Moore 1992, Quigley et al. 1997). During the last 60-80 years western forests have experienced expansion of shade-tolerant firs (Abies) and interior Douglas-fir (Pseudotsuga menzeisii var. glauca) (Monnig and Byler 1992, O'Laughlin et al. 1993). In subalpine forests of the interior northwest, fire suppression, beetle epidemics, and introduced pathogens have contributed to dramatic shifts from shade-intolerant, early successional whitebark pine (Pinus albicaulis Engelm.) to shade-tolerant, late successional subalpine fir (Abies lasiocarpa (Hook.) Nutt.)(Arno and Pederson 1983, Keane et al. 1990, Keane and Arno 1993). Because this subalpine ecosystem is simple in composition and is currently undergoing large-scale successional changes, it provides a good opportunity to investigate successional effects on sapwood:leaf allocation and growth, and changes in forest productivity with age. We compared biomass allocation, growth rate, and growth efficiency between whitebark pines and subalpine firs of different sizes in western Montana.

and extrapolated these measured relationships to whole forests by applying the regression models for individual trees to known size classes of trees in forests ranging in age from 67 to 458 years.

Species

Whitebark pine is a slow-growing, long-lived species common in the subalpine zones and timberline of southwestern Canada and the western United States (Arno and Hoff 1989). It is more abundant on the dry inland slopes of mountains and absent from most of the wettest areas. On very dry sites whitebark pine may form climax stands (Weaver and Dale 1974), but in most forests in which it occurs it is a long-lived seral component of forests that are co-dominated by subalpine fir (Pfister et al. 1977). Subalpine fir is widely distributed in the United States and Canada, and in the subalpine forests of the northern Rockies it is common in the coolest and wettest habitats (Alexander et al. 1990), and in sites too moist for whitebark pine it forms the timberline. The shift from whitebark pine to fir over time is often reset by wildfire, with intervals ranging from 50 to 300 years (Arno 1980). Whitebark pine seeds are dispersed and cached large distances by Clark's nutcracker (Tomback 1982) and is usually the earliest colonist on these burned sites (Arno 1986, Keane et al. 1994). Whitebark pine seeds are a crucial component of the diet of black and grizzly bears, red squirrels, and Clark's nutcrackers (Ferner 1974, Tomback 1982, Mattson et al. 1991). Whitebark pine-dominated forests also protect snowpack in high elevation watersheds and delays snowmelt (Arno and Hoff 1989). Whitebark pine is rapidly decreasing in many parts of its range as a result of mountain pine beetle outbreaks, successional replacement by shade-tolerant subalpine firs,

and the introduced white pine blister rust, Cronartium ribicola (Keane and Arno 1993, Keane et al. 1994).

Site

In order to build regression models for biomass allocation and growth, we harvested 14 whitebark pines and 9 subalpine firs from a ≈5 ha area, at 2300 m elevation, in the Sapphire Mountains of the northern Rockies (46°05'N; 114°50'W) approximately 90 km south of Missoula, Montana, USA. We worked with a smaller sample size for firs because the crown structure of these trees appeared to be highly consistent with dbh and because sapwood:leaf ratios for subalpine fir have been documented elsewhere in the Rockies (Kaufman and Troendle 1981, Margolis et al. 1995). To lessen our impact on beleaguered pristine whitebark communities we chose a site that had already been disturbed in the early 1960's by partial cutting of the overstory trees. For consistency, and to maintain conditions as similar as possible to that in undisturbed forests, we sampled trees within this area that were in closed stands, but with canopies that were not in contact with the canopies of neighbors. By working on a disturbed site and selecting trees that were not densely packed, however, our results probably show higher growth rates and lower sapwood:leaf ratios than trees in dense stands (Dean and Long 1986, Keane and Weetman 1987). The site is on a northwest-facing, 10-15% slope, the substrate is granitic, and mean temperatures for July and January for this habitat type are 14°C and -10°C, respectively (Pfister et al. 1977). None of our sample trees were infected with blister rust.

Methods

Allometry and biomass allocation

Trees of each species were selected to represent their typical ranges of diameters at 140 cm above ground (dbh). Measurements and calculations of allometry and biomass allocation follow Callaway et al. (1994). Total tree height and the basal diameter of all live branches on each bole were measured on trees cut at the base. Three to 5 cm thick transverse disks were cut at 2-m intervals from each bole, and an additional section was cut at the base of the live crown. Disks were stained when necessary with bromecresol green (Kutscha and Sachs 1962) to distinguish sapwood from heartwood and the cross-sectional areas of sapwood, heartwood, and bark on each disk were traced on clear acetate. The area of each component on the acetate was cut out and weighed. Mass of the acetate was converted to area by multiplying by the specific area (in square centimeters per gram) of the acetate. The volume (in cubic meters) of each component in each 2-m bole section was calculated using the areas of the disks at each end of the sections in the following equation: volume = $((A_1 + A_2)/2) \times 2$ m, where A_1 = initial area in square meters and A_2 = terminal area in square meters. Bole volume was calculated by summing all sections for each tree. Volume of each component was converted to mass using the specific gravity (in kilograms per cubic meter) of the heartwood, sapwood, and bark. Specific gravity for each species were determined using known dimensions and dry mass of wood cores and bark cores collected from randomly chosen sections.

Four to five branches were selected randomly and removed from each subalpine fir tree and three to four branches were removed from each whitebark pine. For subalpine firs, each branch was separated into primary branch (the main axis attached directly to the bole),

secondary branches, and leaves. Branches of whitebark pine were often larger and more complex, so each branch was separated into terminal branches (bearing leaves), all other branches, and leaves. Primary branches of firs and all non-terminal branches of pines were cut into 0.5-m long sections, and the diameters of heartwood, sapwood, and the total branch were measured at the end of each cross-section. Cross-sectional areas were calculated from these measurements and volumes were calculated using the previous equation modified for 0.5-m sections. All non-primary branches of firs and terminal branches from pines were collected with the leaves and sorted, dried at 60°C, and weighed. Cross sectional areas of heartwood, sapwood and bark were measured on random subsamples and used to estimate volumes of the smaller branches. Specific weights of the wood and bark of the boles were used to convert secondary branch volumes to the mass allocated to heartwood, sapwood, and bark (see Callaway et al. 1994).

Leaves were removed from each branch, dried at 60°C, and weighed to the nearest gram. Fresh subsamples were chosen from one randomly chosen branch from each tree and measured for one-sided leaf area with MOCHA (Jandel Inc., San Rafael, California, USA) image analysis software. Specific leaf areas (SLA, $m^2 \cdot kg^{-1}$) of the subsamples were used to convert leaf mass to projected leaf area.

Growth Analyses

We measured the width of the five most recent annual rings (1991-1995) for all 23 trees at 3 different places on each disk section. This width was subtracted from all disk sections and bole biomass was recalculated using the 5-year pre-harvest estimates of tree size. The 5-year pre-harvest mass was subtracted from current bole mass for each tree and divided

by 5 to estimate current annual aboveground bole productivity. The annual productivity of the bole, as a percentage of current bole mass, was used to estimate branch productivity. Because whitebark pine allocates proportionally more biomass to branches than subalpine fir with age (see results), this may yield slightly disproportional underestimates of pine productivity. Leaves from ten randomly chosen branches from different trees (in the case of subalpine fir there were only nine sample trees, so one other branch was chosen at random from the entire branch pool) for each species were separated into the sample year's current growth, and that of all previous years, prior to drying and weighing. From this we developed estimates of the proportion of total leaf mass that was a single year's production. This ratio was applied to the canopies of all trees to estimate an annual rate of leaf productivity for each species. Bole, branch, and leaf productivity were summed as an estimate of total aboveground productivity (ANPP) for each species by dbh. We then calculated growth efficiency as grams of wood produced per square meter of projected leaf surface area (Waring 1983).

Projections of allocation and productivity to whole forests

We constructed biomass allocation and ANPP estimates for forests using empirical data from 12 natural stands in the Bob Marshall Wilderness in Montana, 300-400 km north of the harvest site. These stands varied in age from 67 to 458 years old, appeared to have regenerated after stand-replacing fires, and were sampled using standardized ECODATA methodology (Keane et al. 1994). In each stand, 400 m^2 circular plots were located and all tree stems were classified into 5 cm size classes. In each plot 10-20 trees of various sizes, but including the largest trees, were cored as close to the ground as possible and aged by adding

the age at the height of the core to regression estimates for the number of years the tree took to reach core height. To control for variation in microclimate among stands, and to calibrate microclimate between these stands and the harvested stand, we only used stands that were the same habitat type (Abies lasiocarpa-Luzula hitchcockii, Pfister et al. 1977) as the stand used for harvests. Over 95% of the basal area in these stands was whitebark pine and subalpine fir. We entered the median dbh for each dbh class (e.g. 7.5 in the 5-10 cm class) into the regression models that were developed using the harvested whitebark pine and subalpine fir to calculate sapwood mass, leaf mass, and ANPP. Sapwood mass, leaf mass, and ANPP of all dbh classes were summed for each plot and scaled to tM/ha. Time-based models were built using the age of the oldest cored tree in each stand for stand age, which assumed that no trees existed in the stand prior to that time. On average, the oldest subalpine firs sampled in these stands were 45 years younger than the oldest whitebark pines. Therefore whitebark pine and whole-stand allocation and ANPP were extrapolated to time zero and subalpine fir biomass and ANPP to 45 years after time zero. To provide a simple null model for stands without subalpine fir and without recruitment over time, we used the biomass allocation and productivity regressions from harvested whitebark pines to model biomass allocation and productivity of a theoretical, even-aged, whitebark pine stand. This stand began with 400 3.8 cm dbh stems/ha at 50 years (a rounded figure from the two youngest natural stands), experienced 30% mortality every 50 years, and had all surviving trees grow into the next largest age class every 50 years. These inputs were designed so that modeled stands at 450 years in age had similar tree densities in the >50 cm dbh classes to our natural stands that exceeded 400 years in age. Such consistent mortality may be unrealistic for many natural stands, but it is representative of a much larger data set on stand dynamics in the Bob

Marshall Wilderness (Keane et al. 1993).

Statistical Analyses

Whole-tree leaf mass, bole component masses, and branch component masses were regressed on dbh using logarithmic regressions for each species (cf. Whittaker and Woodell 1968, Chapman and Gower 1991, Callaway et al. 1994). Leaf area was regressed against cross-sectional sapwood area at dbh, and sapwood mass:leaf mass ratios and sapwood volume:leaf area ratios were regressed against dbh using simple regression models ($Y = a + bX$) for each species. For small trees that had branches near or to the ground we substituted the diameter at the base for dbh.

For each species, different logarithmic least squares regressions ($\log Y = a - b \log X$) were calculated using branch basal area as the independent variable and total sapwood, total bark, total heartwood, and leaf mass as dependent variables. These regression equations were then applied to all branch bases measured on each tree to estimate total biomass of branch components on whole trees.

To compare biomass allocation at the branch level, leaf area for individual branches was regressed against branch diameter using logarithmic regression models and against cross-sectional sapwood area at the base using simple regressions. Regression models for whitebark pines and subalpine firs were statistically compared for species effects and slope differences using general linear models (GLM) procedures (SAS 1996). Significant species by dbh (or cross-sectional sapwood area at the base of live crown) interactions identified significantly different slopes. To compare patterns of aboveground biomass allocation for whitebark pines and subalpine firs of the same diameters, we used the regressions to develop

models for hypothetical trees of 15 and 50 cm dbh.

Results

Biomass allocation and growth at the tree scale

Subalpine fir trees of all diameters allocated significantly more biomass to leaves and less to sapwood than similar sized whitebark pines (Table 2, Figures 1, 2, 4), but the difference between species was greater for larger trees. Leaf area to cross-sectional sapwood area ratios, measured as the slopes of the regression lines, were 0.66 for subalpine fir and 0.31 for whitebark pine, respectively (Figure 1), and larger individuals of the late-successional species were able to support over twice as much foliage per unit of conducting tissue. For entire trees, sapwood:leaf mass ratios were two to three times higher for whitebark pine than for subalpine fir, depending on the dbh of the trees (Table 2, Figure 2). This was due primarily to much larger volumes of sapwood and low leaf proportions in pine, but also because pine wood density was 0.46±0.01 (1 s.e.) g/cm^3 compared to 0.40±0.01 g/cm^3 for fir. Sapwood volume:leaf area ratios were also much higher for pine (Figure 2), in part due to higher SLA in fir. For leaf cohorts at least one year old, specific leaf area was 3.3 ± 0.3 m^2/kg (1 s.e.) for fir and 3.0 ± 0.2 m^2/kg for pine. We evaluated mass ratios to emphasize the effects of carbon allocation on photosynthetic gain and respiration losses, and volume:area ratios to emphasize the effects of biomass allocation on water relations.

Whole-tree differences in sapwood:leaf ratios were paralleled in the branches (Figure 3, Table 2). The sapwood volume:leaf area ratios of whitebark pine branches increased more rapidly with branch diameter (regression slope = 1.27), than fir sapwood:leaf ratios

(regression slope = 0.27). Whitebark pines also developed larger branches, with models of 50-cm dbh trees allocating over 15% of their total aboveground biomass to branches (Figure 4). In contrast, 50 cm dbh firs allocated only 8% of their aboveground biomass to branches. Allocation patterns within the branches also varied between the species. Of the 138 kg of branches on a modeled 50 cm dbh whitebark pine, 61% of the total mass was sapwood compared to 45% in subalpine fir branches. This appeared to be due, in part, to more extensive development of heartwood in firs (Figure 4).

Canopy architecture differed substantially between firs and pines. A 50 cm dbh subalpine fir was projected by regression models to be 23.6 m tall, and on average supported 32.4±4.5 (1 s.e.) branches per meter of bole. A 50 cm dbh whitebark pine was projected to be 18.2 m tall and only had 15.6±1.2 branches per meter ($t_{species}$ = 4.34, df=21, P<0.001). Low branch density and long branches in this early seral, shade intolerant species seems to maintain an open crown architecture in which light can penetrate throughout the canopy.

Our models of 15 cm and 50 cm dbh trees illustrate the large allocational differences that occur between subalpine fir and whitebark pine, and that these differences are accentuated as trees grow larger (Figure 4). For 15 cm firs, 30% of the entire aboveground biomass exists as leaves and the proportion of leaves decreases to 15% when firs are 50 cm dbh. In contrast, the early successional whitebark pine only allocates 14% of its aboveground biomass to leaves when 15cm dbh, and 8% when 50 cm dbh. Sapwood allocation differences were striking, with the total sapwood mass of a 50 cm fir comprising 29% (257 kg) of its total biomass in comparison to 44% (400 kg) of whitebark pine.

The ANPP of subalpine firs was higher than that of whitebark pines of all ages (Figure 5), and even though subalpine fir had twice the leaf area of whitebark pines, its canopy

growth efficiency was higher than for early-successional whitebark pine (Figure 6). Growth efficiency (kg mass produced per meter of leaf area per year) of firs was similar to that of pines when trees were small, but as trees grew larger the growth efficiency of whitebark pine decreased more rapidly with size than that of subalpine fir ($F_{species} = 8.63$, $P = 0.0081$). The species by dbh interaction was not significant. Growth efficiency differences were reflected in comparisons in ANPP (leaves and wood combined), as firs of all sizes produced significantly more mass per year than pines (Figure 5). Age-dbh regressions were consistent with measurements of growth efficiencies (Figure 7), but the age by species interaction was not significant ($F=2.66$, $P=0.12$), indicating no significant difference in the regression slopes.

Biomass allocation and productivity at the whole-stand level

Reconstruction of stand biomass allocation from field data suggested that subalpine fir maintained a substantially lower whole-forest sapwood:leaf ratio than would be predicted from the biomass allocation of either even-aged stands or naturally developing stands of whitebark pine (Figures 8, 11). Unlike whitebark pine, for which sapwood:leaf ratio was high and continued to increase throughout our range of forest stand ages, subalpine fir populations maintained very low and stable sapwood:leaf ratios throughout the 450 year seral sequence. This was because individual subalpine firs increased sapwood:leaf ratios slowly with dbh (Figure 2) and many young firs became established late in stand development, even the oldest stands (Figure 9). For example, in the two oldest stands (406 and 458 years), there were 410 and 470, respectively, individual subalpine firs in the 1-5 cm size class per hectare and 180 and 160 individuals/ha in the 5-10 cm size class. Based on the growth rates from our harvested trees, these firs were estimated to contribute an average of 20% of the ANPP of

these two stands.

Our empirical models suggest that the maintenance of low stand sapwood:leaf area ratios, and a favorable balance of respiration and assimilation, by subalpine fir has the potential to maintain high rates of stand productivity even in forests more than 400 years old (Figure 10). The contrast is illustrated by comparing whole-stand ANPP in the natural forests to the general pattern of productivity over time in our null model ANPP (Figure 11). The latter shows the classic pattern of rapid increases in ANPP and then decreasing ANPP as sapwood:leaf ratios continue to rise. In the natural forests, ANPP of whitebark pine declined in the oldest stands, but high growth rates and recruitment rates of late-successional subalpine fir sustained gradually increasing rates of whole-stand ANPP for this species during the 450 year span of our sample stands. The role of subalpine fir in maintaining stand ANPP is evident in comparisons of the proportional contribution of each species to stand productivity at different stand ages. In the three youngest stands, whitebark pine contributed 67% of the stand productivity, but the three oldest stands the trend was reversed with subalpine fir contributing 62% of the whole-stand productivity.

Discussion

Subalpine forests in our study appear to sustain continued, gradual increases in ANPP over three to four centuries. Even at 400-450 years we found no evidence for a decline in productivity. Late-successional subalpine fir appeared to play a major role in maintaining low sapwood:leaf ratios and productivity as stands aged. These findings support others that indicate that evergreen conifer forests may remain highly productive for centuries. Weaver

and Dale (1974) estimated that stands dominated by whitebark pine in drier environments than studied here gradually increased in productivity over several hundred years. Grier and Logan (1977) estimated ANPP of 450 year-old Douglas-fir-western hemlock forests in the northwest USA at 10.8 $tM \cdot ha^{-1}yr^{-1}$, whereas ANPP in 100 year-old and 150 year-old stands was estimated at 12.7 and 9.5-10.5 $tM \cdot ha^{-1}yr^{-1}$ respectively (Fujimori et al. 1976, Gholz 1982). Pacific-silver fir (Abies amabilis) stands measured by Grier et al. (1981) only decreased from 6.4 to 4.6 $tM \cdot ha^{-1}yr^{-1}$ over 157 years. However, these productivity rates do not integrate the effects of tree mortality over time (as do ours). DeBell and Franklin (1987) argued that biomass loss to mortality may roughly equal that gained by net productivity in old Douglas-fir – western hemlock forests, but estimates of annual biomass lost as "coarse woody debris" in mature to old northwestern forests are extremely variable and range from 0.5 to 30.0 $tM \cdot ha^{-1}yr^{-1}$ (Harmon et al. 1986). We applied the mortality coefficient estimated by Turner et al. (1995) for Douglas-fir and spruce-fir forests in the Rocky Mountains (0.50% of standing biomass) to the total biomass of forests in the studies cited above and calculated that 3.6-4.4 $tM \cdot ha^{-1}yr^{-1}$ of biomass should be lost to mortality. The differences between ANPP and mortality suggest that even old stands of a number of different forest types may maintain substantial positive rates of productivity.

In our study, productivity may have been sustained because late-successional, shade-tolerant subalpine fir had much lower apparent respiration:assimilation ratios, higher growth rates, and higher growth efficiencies than early-successional whitebark pines. Our calculations of the projected leaf area to sapwood cross-sectional area ratio for subalpine firs (0.66) was similar to that determined in other forests (0.75, Kaufman and Troendle 1981, Margolis et al. 1995). Leaf area is highly correlated with stand productivity in many other

forest types (Fassnacht and Gower 1997). Our projections of size-based regression models to whole stands supports the hypothesis that successional species replacement in these forests maintains favorable assimilation to respiration ratios and high ANPP for much longer than would be predicted by simple trajectories of sapwood:leaf ratios of single species or even-aged stands. As environmental conditions change over time such that subalpine fir is favored, both fir recruitment over long time periods and low rates of sapwood accumulation for individual fir trees contribute high proportions of assimilatory tissue and low proportions of heterotrophic tissue at the stand level.

We caution that our calculations of growth rates and growth efficiencies may be higher than for other, similar stands for two reasons. First, we harvested trees from stands that had been thinned 30 years before our study, and increases in the widths of the annual rings of some of the harvested trees indicated that they may have been released from competitive inhibition. Others have shown that canopy position or stand density can affect sapwood:leaf ratios (Pearson et al. 1984, Keane and Weetman 1986, Dean and Long 1986, Hungerford 1986, Naidu et al. *in review*). The annual growth increment at dbh of subalpine fir and whitebark pine harvested for this study averaged 2.20±0.50 mm (1 s.e.) and 1.20±.40 mm, respectively. These are substantially higher than those we have collected from other old subalpine forests in the region. Annual increments at dbh from whitebark pines and subalpine firs from three other stands between 2200 and 2400 m elevation ranged from 0.44±0.05 to 0.61±0.11 for firs and 0.18±0.11 to 0.22±0.06 for pines (Callaway, *in press*). This suggests that our estimates of whole-stand productivity may be several times higher than that in many other subalpine forests dominated by these species. However, the greater differences between whitebark pine and subalpine fir growth rates in these other forests (Callaway, *in press*)

suggests that whitebark pine in other forests may show an even more rapid proportional drop in growth relative to fir than predicted by our models, and there may be a greater relative effect of subalpine firs on the maintenance of productivity over time.

A second caveat is that our regression models are built from pines that that did not exceed 228 years in age and firs that did not exceed 140 years. These regressions were used to predict stand allocation and growth for pines up to 458 years old and firs up to 263 years old. These discrepancies in age probably do not have large effects on our estimates of forest biomass allocation because allocation is strongly related to tree size, rather than age, and are reasonable for *relative* comparisons of species-specific effects on forest productivity. In our two oldest stands, 28% of the productivity of whitebark pine, and none of the productivity of subalpine fir (the oldest fir was in a middle-aged stand), could be attributed to trees outside of the age limits of our regressions. Thus, even conservative estimates of forest productivity would still show substantial biomass accumulation in the oldest forests. Our estimates of stand productivity overlap with tables of yield capability determined by Pfister et al. (1977). Their estimates of stand (bole) ANPP for this forest type ranged from 0.1 to 0.7 $tM \cdot ha^{-1}yr^{-1}$. Our estimates ranged from approximately 0.5 to 2.5 $tM \cdot ha^{-1}yr^{-1}$ which is low compared to other types of forests (Waring and Schlesinger 1985, Franklin 1988, Peet 1988). However, we included leaf and branch ANPP, which roughly doubled estimates for boles. Furthermore, our calculations explicitly included measurements of growth in the upper bole, which was greater than growth at dbh, the height at which conventional bole growth rates are determined.

Our data may also overestimate the contribution of new recruits to whole-stand ANPP. The smallest subalpine firs and whitebark pine in our harvest did not appear to be as

suppressed as those in stands sampled for whole-stand allocation. In the 12 stands sampled in the Bob Marshall wilderness, the average ages of firs and pine 2.5-5 cm dbh were 65.4±7.1 (1 s.e.) and 75.5±10.0, respectively. The 4-10 cm dbh trees in our harvest were 20-70 years old. Our predictions of the contribution of young firs to whole-stand ANPP are too high when small individuals are more suppressed than those used in our harvest-based models.

Due to harsh physical conditions, canopy closure may be more gradual in subalpine forests than in lower elevation forests, and gradual canopy closure may create opportunities for continuous recruitment that may not occur in other forests (Peet 1980). If other types of forests show substantially less recruitment after initial stand establishment than we and others (Tomback et al. 1993, Callaway, *in press*) have observed for subalpine forests, the effects of succession on whole-stand biomass allocation will be less. Recruitment over time is highly variable among forest types, and varies even among similar subalpine forests of the Rockies (Peet 1988). However, there is extensive evidence for recruitment of trees long after stand initiation in many coniferous forests including those dominated by Pseudotsuga menzeisii and Tsuga heterophylla (Franklin and Hemstrom 1980, Huff 1995), Pinus strobus and Tsuga canadensis (Abrams and Orwig 1996), and mixed species in the northern Rocky Mts. (Arno et al. 1997). Even though these forests, and ours, show distinct differences in proportional abundance either early or late after stand initiation, it should be noted that none of these forests follow a strict pattern of relay floristics and "early" and "late" successional species may be found in forests of many different ages.

In our subalpine community, late-successional subalpine fir grew at higher rates than early-successional whitebark pine. This pattern may not hold in other forests, especially those in more mesic or moderate climates. Horn (1971, 1974) argued that early successional trees

were intrinsically more productive than late successional trees, and some data from southeastern forests supports this (Peet 1980). On the other hand, late-successional Pinus strobus and P. resinosa appear to maintain high stand productivity in 60-70 year-old forests in Michigan (Cooper 1980). However, late successional species may maintain high rates of productivity in forests even if they grow more slowly than the species that precede them because young trees have higher growth rates than old trees.

Our models of stand allocation and growth were also affected by recent whitebark pine mortality due to the non-native whitebark pine blister rust. The basal area of dead whitebark pines averaged 13% of the total basal area over all stands (R.E. Keane, unpublished data), but some mortality was natural and not due to blister rust. Mortality due to blister rust is much more common for larger pines, and because larger trees always have higher sapwood:leaf ratios, our estimates of whitebark pine sapwood:leaf ratios in old stands may have been low in comparison to stands without blister rust. Therefore our calculations of the proportional contribution of firs to sapwood:leaf ratios in old stands may be high. High mortality rates of large pines due to non-native factors certainly introduce underestimates of stand ANPP and the contribution of pine to ANPP. However, we could not detect any systematic relationship between whitebark pine mortality and stand productivity as the percent basal area of dead whitebark pine in stands was not correlated with either total stand ANPP ($r = 0.37$, $P = 0.24$) or the proportion of ANPP attributed to firs ($r = 0.01$, $P = 0.97$). However, virtually all whitebark stands in northern Montana, Idaho, and Washington are experiencing mortality due to blister rust which appears to be accelerating the conversion of these forests to subalpine fir.

Our results support the general evidence in the literature for high sapwood:leaf ratios of species that dominate soon after stand initiation and low ratios of species that dominate old

forests (Table 1). To our knowledge, only one other study has directly compared intermixed early- and late-successional species at the same site, and whole-tree aboveground biomass allocation was not compared. As in this study, Kaufman and Troendle (1981) found that early successional lodgepole pine (Pinus contorta) and late-successional subalpine fir in Colorado had sapwood cross-section area:leaf area ratios of ≈ 0.18 and ≈0.75 (after corrections to projected leaf area, see Waring and Schlesinger 1985), respectively. However they harvested trees over a wide range of sites and 300 meters of elevation, which confounded site effects with successional effects on allocation.

Correlations between sapwood:leaf ratios and the successional status of conifers has not been considered explicitly in the literature, but it is not surprising. Large-scale and gap-scale disturbances may create hotter and perhaps drier conditions (Geiger et al. 1995) which can favor species that have the ability to store large amounts of water in their tissues. Conversely, once early successional trees have established, the forest floor often becomes more mesic and light levels decrease. These conditions favor species that allocate proportionally more biomass to leaves (Waring and Schlesinger 1985, but see Naidu et al. *in review*) and long-term water storage capacity may not be as essential. We correlated sapwood:leaf ratios reported for a number of species in the literature with their reported light compensation points and shade tolerance rankings (after Wenger 1984)(Figure 12). We found that sapwood:leaf ratios were highly negatively correlated with shade tolerance, indicating that the general allocational differences reported here for whitebark pine and subalpine fir may occur in other forests. However, we caution that fir contributed to low sapwood:leaf ratios and high productivity via species-specific allocation patterns and by long-term recruitment of young individuals even in the oldest stands. If other forests do not undergo

similar recruitment patterns, late-successional species there may not be effective at maintaining low respiration:assimilation ratios.

The relationship between leaf area and productivity we found for subalpine fir and whitebark pine commonly occurs in other forest types. Fassnacht and Gower (1997) reported correlations between leaf area index and aboveground net primary production for forests in central Wisconsin and organized similar results from 8 other studies. Maximum leaf area index is also tightly correlated with sapwood production in forests of east-central Washington (Schroeder et al. 1982). Thus it is reasonable that increasing leaf area with successional shifts in forests should be associated with increases in productivity. Ultimately, however, self-shading, aging late-successional species, and increasing numbers of suppressed individuals should develop unfavorable respiration:assimilation ratios and place upper limits on ANPP (see Waring 1983). Our results, however, indicate that these upper limits may occur in much older forests than currently thought.

The differences in biomass allocation between whitebark pine and subalpine fir corresponds with their different roles in forest development over time. Both of these species are present on sites soon after disturbance; for all stands in the Bob Marshall Wilderness, the oldest whitebark pines averaged only 45 years older than the oldest subalpine fir. However, whitebark pine typically dominates younger stands and regenerates poorly once canopies are dense (Figure 9, Arno and Hoff 1989). Whitebark pine has a much higher water storage capacity in sapwood than subalpine fir, giving it an advantage in open, moisture limited sites. However, the respiration costs of maintaining such high sapwood biomass may prevent whitebark pine from long-term persistence in the subcanopy. In contrast, high leaf areas and low respiration costs may contribute to the ability of subalpine fir to recruit in the understory

in established forests.

We have emphasized the potential for long-term productivity in these subalpine forests; however, fire is an integral part of this ecosystem and occurs at 50 to 300 year intervals (Arno 1980). These fires are often stand-replacing (Losensky 1990). Whitebark pines have a dispersal advantage after large fires because Clark's nutcrackers (Nucifraga columbiana) cache whitebark pine seeds great distances into burns (Tomback et al. 1990). Subalpine fir experiences much higher mortality in light ground fires compared to whitebark pine, and natural fire regimes in these forests are likely to maintain forests dominated by whitebark pine (Arno 1986, Arno and Hoff 1989). As ecosystems convert to subalpine fir due to fire exclusion and blister rust, increases in allocation to leaf area, and the much higher transpiration rates of fir (Smith et al. 1997*b*, R.M. Callaway, unpublished data) may have detrimental effects on watershed processes in addition to their effects on carbon budgets (Keane et al. 1996).

Our finding that sapwood:leaf ratios may be lower in old forests than currently recognized should be integrated with recent studies that show that respiration rates per sapwood volume decrease with tree age and size. Ryan (1990) found that the total respiration rates of Englemann spruce (Picea englemanii), also a common subalpine species in the northern Rockies, decreased with tree diameter. Maintenance respiration of ponderosa pine also decreases with tree size in mesic and xeric environments (Carey et al. 1997). In boreal forests, old jack pine (Pinus banksiana) stands had lower maintenance respiration rates per unit sapwood than young stands (Lavigne and Ryan 1997). Ryan and Waring (1992) found that the maintenance respiration rates (per unit ground area) of a 40 year-old stand of subalpine Pinus contorta (61 $g \cdot m^{-2} \cdot yr^{-1}$) did not differ from that of a 245 year-old-stand (79

$g \cdot m^{-2} \cdot yr^{-1}$) and could not explain the dramatic decline they observed in wood production. In general, maintenance respiration appears to account for only 5 to 12% of carbon fixation for most forests (Ryan et al. 1995). These data, and the alternative hypotheses for age-related declines in forest productivity explored by Murty et al. (1996), Ryan et al. (1997), and Ryan and Yoder (1997) demonstrate a need to re-evaluate the mechanisms that determine forest productivity over time, and the models that are currently used to estimate forest productivity at regional and global scales.

Aboveground carbon sequestering in forests is a product of carbon gained as ANPP and carbon lost due to mortality and decomposition (net ecosystem productivity, Turner et al.1995). Although our time sequence of stands incorporates mortality, we applied the mortality coefficient of Turner et al. (1995) for spruce-fir forests in the Rocky Mountains (0.50%) to the total biomass of the oldest forest that we studied to estimate the potential for mortality to cause underestimates in carbon sequestering. We calculated that roughly 0.5 $tM \cdot ha^{-1}yr^{-1}$ of biomass should be lost to mortality. This is a relatively small proportion of the approximately 1.5-2.5 $tM \cdot ha^{-1}yr^{-1}$ that old stands produced and suggests that even the oldest stands may be carbon sinks. As a further precaution against misinterpreting the effects of ANNP on carbon acquisition in these stands we used DBH-total tree biomass regressions to estimate changes in biomass of living trees in stands over time and found that biomass accumulation also continued to increase until approximately 400 years (Figure 13).

Direct comparisons of productivity of forests of different specific ages are rare in the literature (see Ryan et al. 1997) and the theoretical connections between specific forest ages, biomass allocation, net *ecosystem* productivity (see Turner et al. 1995), and net annual productivity in forests is vague and there appear to be strong regional differences (Turner et

al. 1995). However, this theoretical connection plays an important role in the harvesting of public and private forests (Smith et al. 1997*a*) and estimates of global carbon budgets (Melillo et al. 1995). For example, Mellilo et al. (1995) state that "old-growth forests accumulate little if any carbon" and that only forests that are re-growing from cutting in the early to mid-1900's are accumulating significant amounts of carbon. Clearly, overestimating the rate at which the productivity of old forests declines will underestimate the potential of old forests to sequester atmospheric carbon. The perception that mature forests are not productive, and thus do not do their part in the global carbon crisis, has even led to Congressional proposals to harvest and replace them with young forests (see Harmon et al. 1990). Coniferous forests cover 24% of the terrestrial surface of the globe and are especially important because they store large amounts of carbon at mid- to high- latitudes where the consequences of climate change are likely to be the greatest (Houghton et al. 1991, Gucinski et al. 1995). Conifer biomes have the potential to affect feedback among biosphere carbon fluxes and storage (Neilson and King 1992), but many models of carbon storage and flux for conifer forests do not account for succession as described here (see Dixon et al. 1994). Sedjo (1992) argued that temperate forests are an important global carbon sink, and primarily based his argument on recent forest expansion and re-growth. If successional shifts maintain low sapwood:leaf ratios and productivity in coniferous forests, such as described here for subalpine forests, old forests may contribute to the role of temperate forests or "northern land biota" as a "missing sink" (Kauppi et al. 1992, Sedjo 1992, Ciais e al. 1995, Keeling et al. 1996). Our results indicate that successional effects on long-term productivity of forests should be considered in global climate models. However, before we can conclude that succession maintains higher rate of productivity and carbon storage in forests in general, much more evidence from other forest

types is necessary.

In summary, shade-tolerant, late-successional subalpine fir appears to maintain low sapwood:leaf ratios in subalpine forests via inherently low sapwood:leaf area of individual trees, low rates of increase in sapwood:leaf ratios (lower regression slopes) with size, and high recruitment rates over hundreds of years of stand development. In general, late-successional and shade-tolerant species have relatively low sapwood:leaf ratios suggesting that temporal patterns reported here for subalpine forests may occur in other forests. The effects of succession on maintaining productivity should be measured in other forests, and if late-successional species are found to maintain favorable sapwood:leaf ratios in other ecosystems, we may be greatly underestimating the productivity and carbon storage potential of old forests.

Acknowledgments

We thank Erick Aschehoug, CT Callaway, Andrew Carroll, Trevor Laboski, Kevin Murray, and Jodee Smith for enduring long days in the field, mosquitoes, cheap beer, and chainsaw injuries to collect data for this paper. We are also indebted to Troy Byker, Todd Carlson, Scott Mincemoyer, and Toby Palm for long hours of branch sorting and weighing. Thanks to Steve Arno, Eileen Carey, Dan Leavell, and Kevin O'Hara for reading and evaluating the manuscript. This work was supported by the USDA Forest Service, Rocky Mountain Research Station, INT-95086-RJVA to R. Callaway and A. Sala and USDA NRIGCP 95-37101-1683 to R. Callaway.

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Table 1: Ratios of projected leaf area to sapwood cross-sectional area for early and late successional conifer species pairs in the northern Rocky Mountains. Biomass ratios are taken from Waring and Schlesinger (1985), Kimmins (1987), Callaway et al. (1994), Margolis et al. (1995), Successional trends are taken from Pfister et al. (1977, Appendix B).

Early Succession (m^2/cm^2)		Late Succession (m^2/cm^2)
Pinus ponderosa (.17-.25)	→	Pseudotsuga menziesii (.25-.70)
Pinus ponderosa (.17-.25)	→	Abies grandis (.51)
Pinus contorta (.11-.30)	→	Pseudotsuga menziesii (.25-.38*)
Pinus contorta (.11-.30)	→	Abies lasiocarpa (.75)
Pinus contorta (.11-.30)	→	Tsuga heterophylla (.46)
Pseudotsuga menziesii (.25-.38*)	→	Abies lasiocarpa (.75)
Pseudotsuga menziesii (.25-.38*)	→	Abies grandis (.51)

* Pseudotsuga menzeisii is highly variable in sapwood:leaf ratios. Here we report ratios for the interior variety, (P. menzeisii. glauca), the interior, coastal varieties (var. Douglasii) have much higher ratios.

Table 2. Regression models for biomass allocation among sapwood, bark, heartwood, leaves, and height for subalpine fir and whitebark pine in western Montana

		Regression model	r^2
Leaf mass (LM)◆	Subalpine fir	logLM = -1.170 + 1.949(logdbh)	0.98
	Whitebark pine	logLM = -1.409 + 1.925(logdbh)	0.98
Bole sapwood (BSW)◆	Subalpine fir	logBSW = -1.634 + 2.349(logdbh)	0.99
	Whitebark pine	logBSW = -1.599 + 2.412(logdbh)	0.99
Bole heartwood (BHW)◆*	Subalpine fir	logBHW = -2.351 + 2.902(logdbh)	0.99
	Whitebark pine	logBHW = -3.525 + 3.570(logdbh)	0.94
Bole bark (BB)◆	Subalpine fir	logBB = -2.036 + 2.328(logdbh)	0.98
	Whitebark pine	logBB = -1.754 + 1.951(logdbh)	0.94
Total branch sapwood (BrS)◆*	Subalpine fir	logBrS = -2.195 + 2.163(logdbh)	0.96
	Whitebark pine	logBrs = -3.161 + 2.994(logdbh)	0.94

Table 2 cont.

Total branch heartwood (BrHW)◆*	Subalpine fir	logBrHW = -2.778 + 2.266(logdbh)	0.95
	Whitebark pine	logBrHW = -4.498 + 3.384(logdbh)	0.95
Total branch bark (BrB)◆*	Subalpine fir	logBrB = -1.779 + 1.836(logdbh)	0.98
	Whitebark pine	logBrB = -1.754 + 1.951(logdbh)	0.94

* equations with significantly different slopes (significant species by dbh interactions in GLM)

◆ equations with significant species effects in GLM.

Figure Legends

Figure 1. Whole-tree projected leaf area (LA) versus cross-sectional sapwood area (SA) at dbh for subalpine fir and and whitebark pine in subalpine forests of western Montana. For subalpine fir, LA = -1.28 +0.66(SA), $r^2 = 0.97$. For whitebark pine LA = -10.86 + 0.31(SA), $r^2 = 0.94$. Slopes differed significantly, GLM, $F_{SA \times species} = 56.56$, $P < 0.0001$.

Figure 2. Whole-tree relationships between sapwood and leaves for subalpine and whitebark pine in western Montana. (a) Whole-tree leaf area:sapwood volume ratios (SLR) versus dbh. For subalpine fir SLR = 917.4 – 15.1 (dbh), $r^2 = 0.75$. For whitebark pine SLR = 388.2 – 6.0 (dbh), $r^2 = 0.70$. Slopes differed significantly, GLM, $F_{dbh \times species} = 9.91$, $P = 0.0053$. b) Whole-tree sapwood mass:leaf mass (SLM) versus dbh for subalpine firs and whitebark pines. For subalpine fir SLM = 1.271 – 0.020(dbh), $r^2 = 0.77$. For whitebark pine SLM = 0.541 – 0.009(dbh), $r^2 = 074$. Slopes differed significantly, GLM, $F_{dbh \times species} = 14.48$, $P = 0.0012$.

Figure 3. Relationships between sapwood volume:leaf area ratios (BSV) and branch diameter (BD) for individual branches of subalpine fir and whitebark pine in western Montana. For subalpine fir BSV = -0.77 +0.27(BD), $r^2 = 0.09$. For whitebark pine BSV = -2.01 + + 1.27(BD), $r^2 = 0.74$. Slopes differed significantly, GLM, $F_{BD \times species} = 8.95$, $P = 0.0037$.

Figure 4. Biomass allocation of simulated trees of subalpine fir and whitebark pine with 15 cm and 50 cm dbh. Predicted values were derived from regression equations for dbh and sapwood, heartwood, bark, and leaf values. Regression equations are presented in Table 2. Percents in parentheses are of total aboveground biomass.

Figure 5. Whole-tree annual net primary productivity (ANPP) versus dbh of subalpine fir and whitebark pine in western Montana. For subalpine fir, log(ANPP) = -1.870 + 0.1.903(logdbh), $r^2 = 0.99$. For whitebark pine log(ANPP) = -2.080 + 1.788(logdbh), $r^2 = 0.98$. Slopes did not differ significantly, but the effect of species did. GLM, $F_{species} = 100.47$, $P < 0.0001$.

Figure 6. Whole-tree growth efficiency (E) versus dbh of subalpine fir and whitebark pine in western Montana. For subalpine fir, E = 0.0571 - 0.0002(dbh), $r^2 = 0.50$. For whitebark pine E = 0.0545 - -0.0003(dbh), $r^2 = 0.43$. Slopes did not differ significantly, but the effect of species did, GLM, $F_{species} = 8.63$, $P = 0.0081$.

Figure 7. Age versus dbh of subalpine fir and whitebark pine in western Montana. For subalpine fir, DBH = -7.147 + 0.306(age), $r^2 = 0.91$. For whitebark pine DBH = -5.132 + 0.223(age), $r^2 = 0.84$. Slopes did not differ significantly (age by species interaction, F=2.66. P=012).

Figure 8. Whole-stand sapwood:leaf mass ratios for 12 subalpine forest stands of different ages in the Bob Marshall Wilderness. Curves were fit as 2nd order regressions.

Figure 9. Size class distributions for whitebark pine and subalpine fir in (a) the three youngest, (b) four stands of intermediate age, and (c) the two oldest stands sampled in the Bob Marshall Wilderness.

Figure 10. Whole-stand annual productivity rates for 12 forest stands of different ages in the Bob Marshall Wilderness. Figure 8. Curves were fit as 2nd order regressions.

Figure 11: Simulated whitebark pine stand productivity and biomass allocation without subalpine fir and without recruitment over time. This model used regressions from harvested whitebark pines to model biomass allocation and productivity of a theoretical whitebark pine stand over 450 years. This stand began with 400, 3.8 cm dbh stems/ha at 50 years (derived from the two youngest natural stands), experienced 30% mortality every 50 years, and had all surviving trees grew into the next largest age class every 50 years. These inputs were designed so that modeled stands at 450 years in age had similar tree densities in the >50 cm dbh classes to our natural stands that exceeded 400 years in age. Figure 8. Curves were fit as 2nd order regressions.

Figure 12. (a) Means and 95% confidence limits for leaf:sapwood ratios for shade-tolerant and shade-intolerant evergreen conifer species. Shade-tolerant bar includes species from the "very-tolerant", "tolerant", and "intermediate" classes of Wenger (1984), and the shade-intolerant bar includes species from the "intolerant" and "very intolerant" classes. (b) Regression relationship between light compensation point (percent of full sunlight) and leaf area:sapwood cross-sectional area ratios for evergreen conifer species. Species used were Abies grandis[1,2], Abies lasiocarpa[1,3,4], Picea abies[1,2], Picea englemanii[1,2], Pinus albicaulis[3,4], Pinus contorta[1,2], Pinus ponderosa[1,2], Pinus svlvestris[1,2], Pseudotsuga menziesii[1,2],

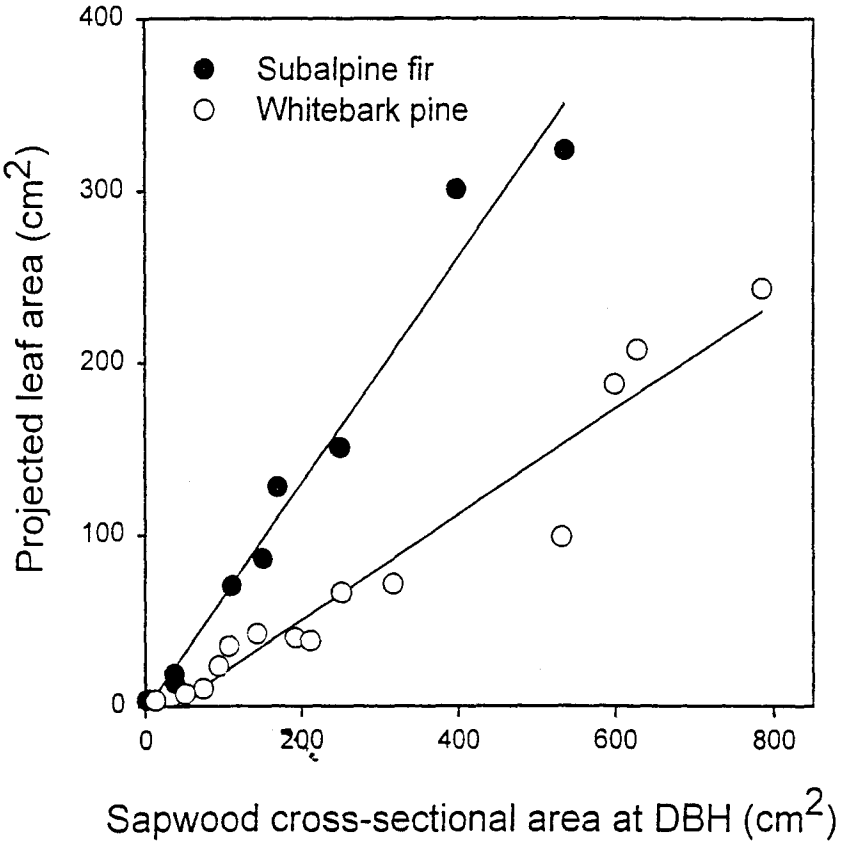
[1] leaf:sapwood ratio from Margolis et al.(1995).

[2] compensation point from Kimmins (1997).

[3] leaf:sapwood ratio from this study, or data from this study average with others.

[4] compensation point from R.M. Callaway, unpublished data.

Figure 13. Whole-stand biomass for 12 forest stands dominated by whitebark pine and subalpine fir of different ages in the Bob Marshall Wilderness. Figure 8. Curves were fit as 2nd order regressions.


Subalpine fir
Whitebark pine
Projected leaf area (cm2)
Sapwood cross-sectional area at DBH (cm2)
0
100
200
300
400
0
200
400
600
800

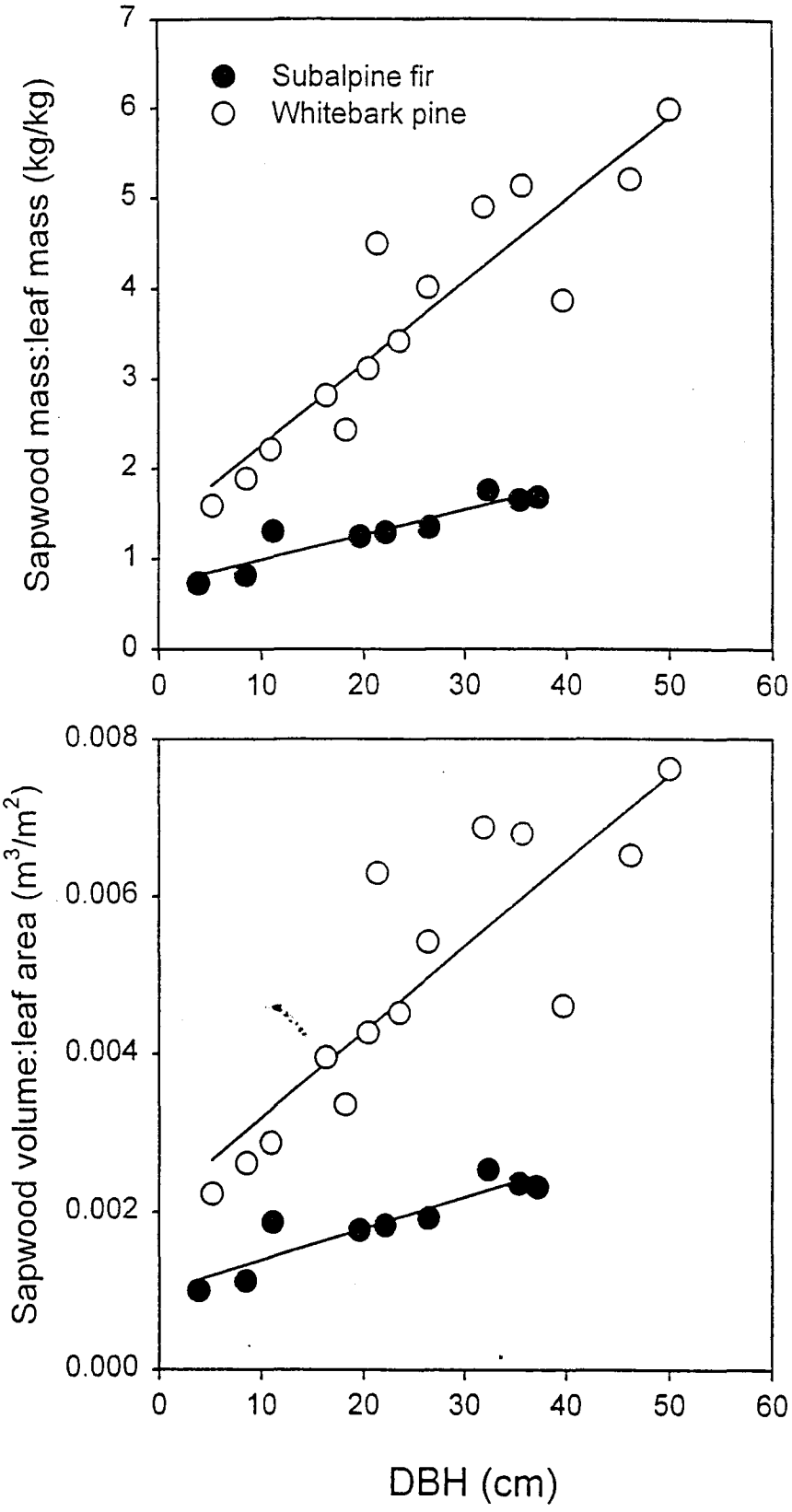

Subalpine fir
Whitebark pine
Sapwood mass:leaf mass (kg/kg)
Sapwood volume:leaf area (m3/m2)
DBH (cm)
0
1
2
3
4
5
6
7
0.000
0.002
0.004
0.006
0.008
0
10
20
30
40
50
60

Fig. 2

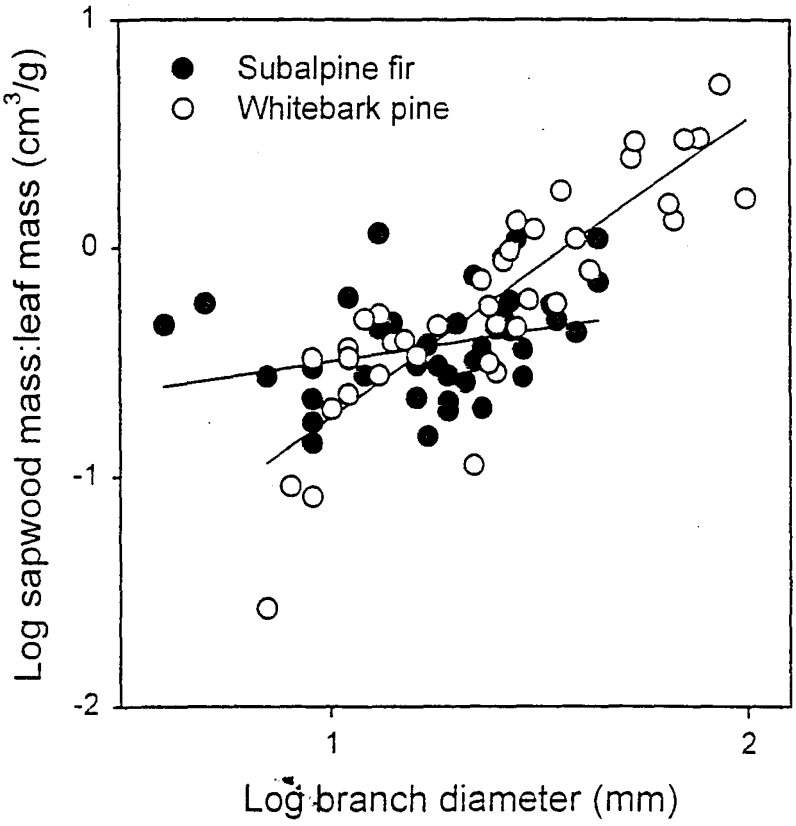
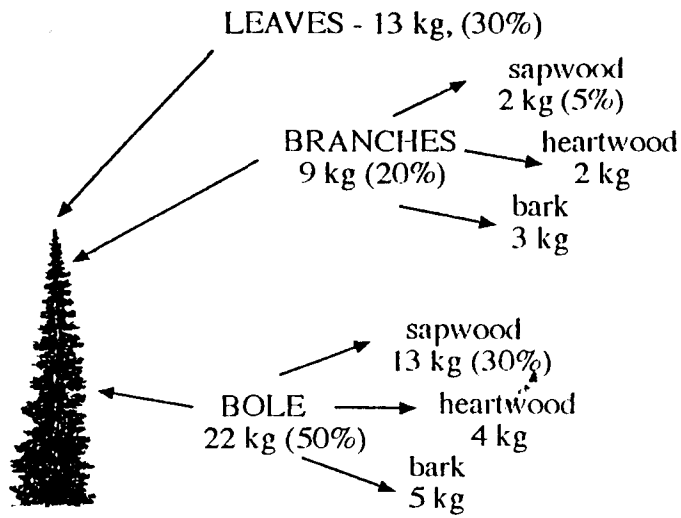
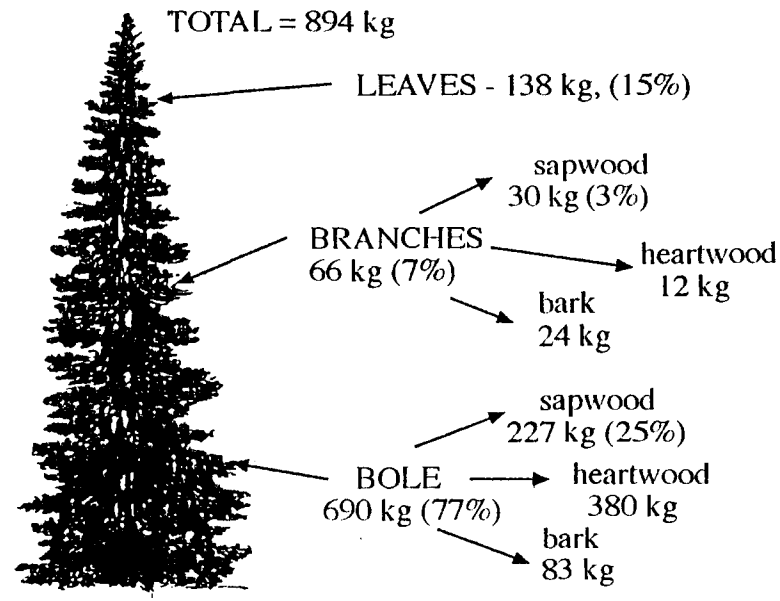

Subalpine fir
Whitebark pine
Log sapwood mass:leaf mass (cm3/g)
1
0
-1
-2
1
2
Log branch diameter (mm)

Fig. 3

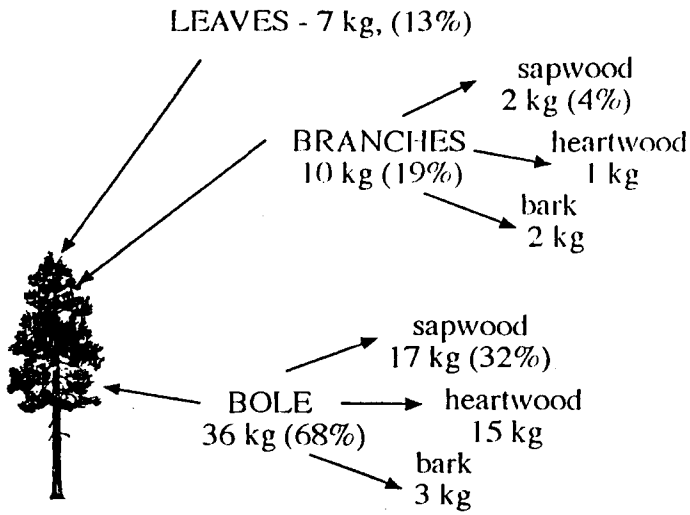
TOTAL = 44 kg



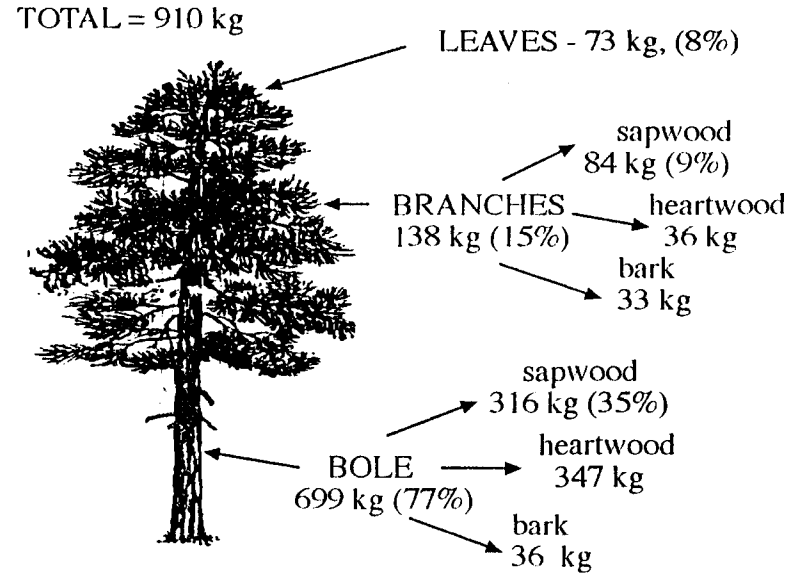
TOTAL = 894 kg



TOTAL = 53 kg



TOTAL = 910 kg



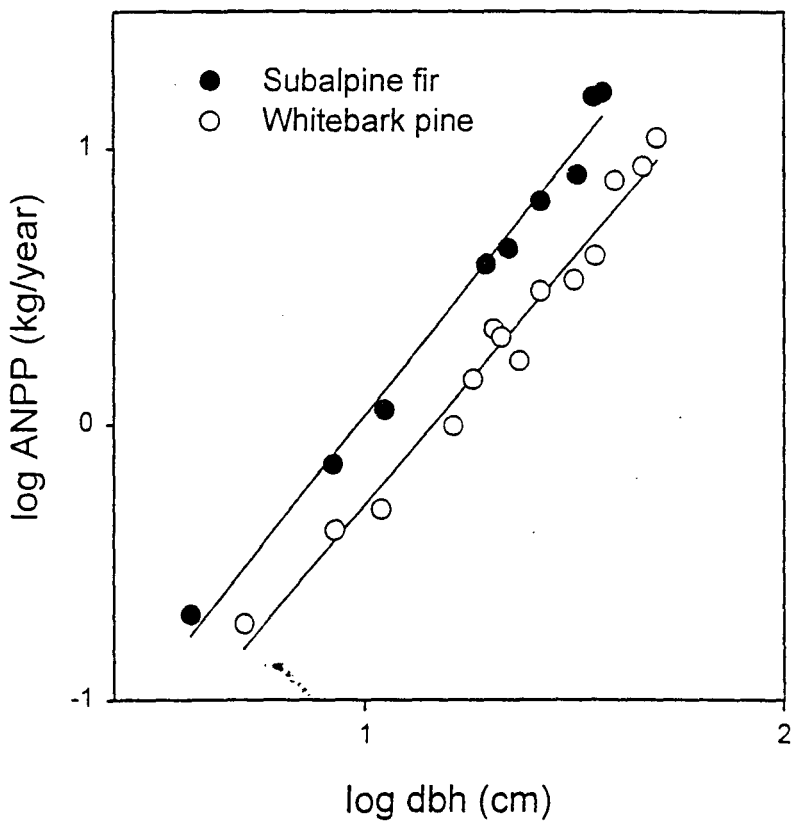
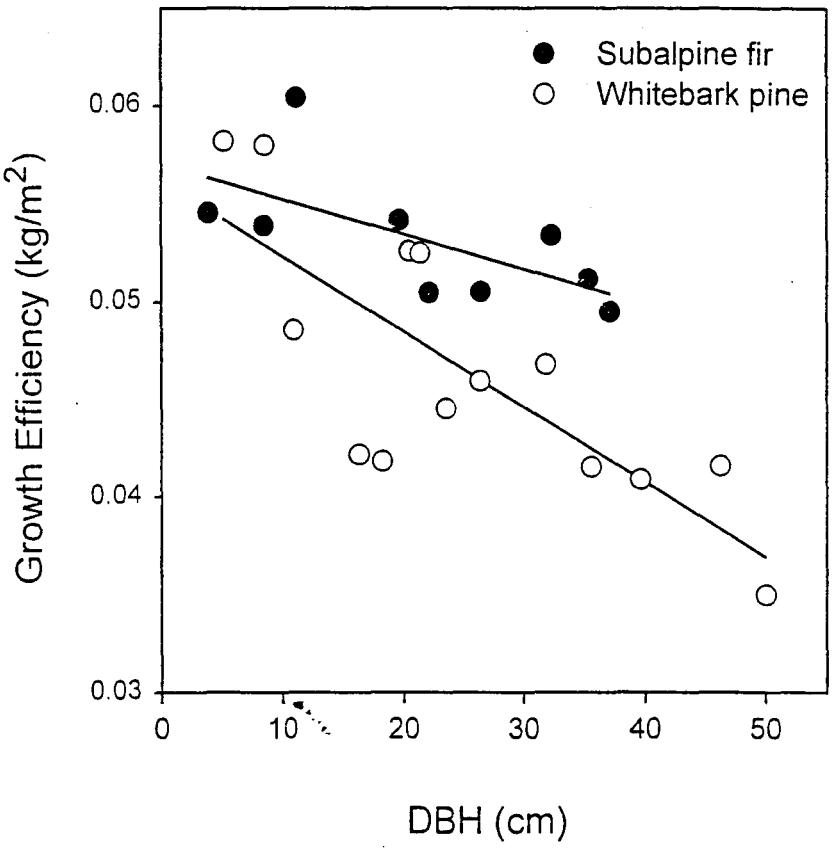
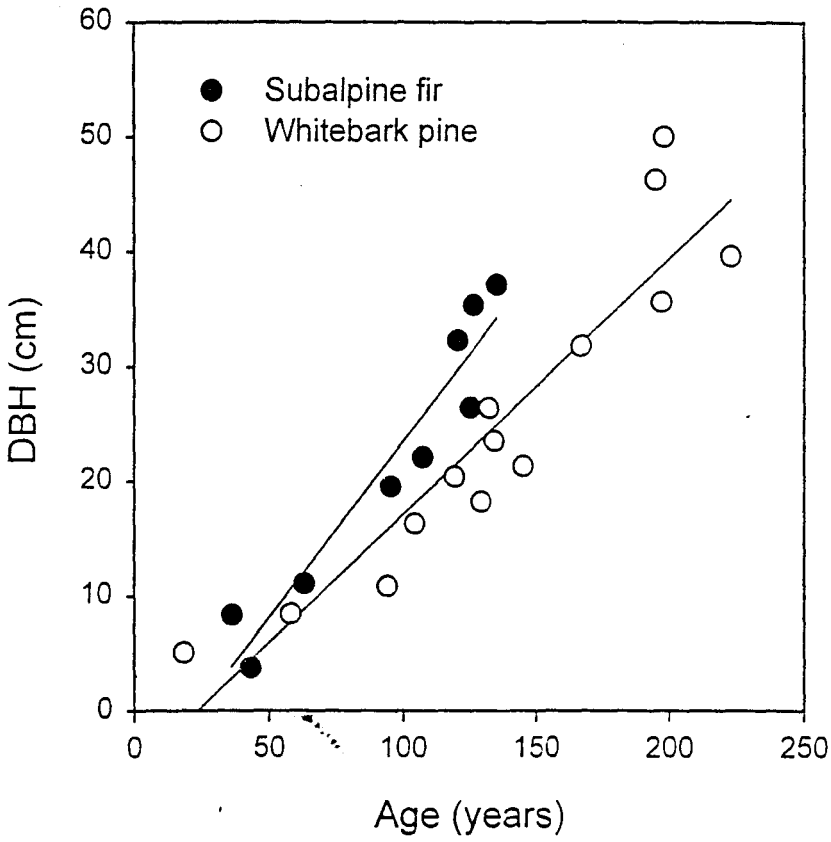

Subalpine fir
Whitebark pine
log ANPP (kg/year)
1
0
-1
1
2
log dbh (cm)

Fig. 5


Subalpine fir
Whitebark pine
Growth Efficiency (kg/m2)
0.06
0.05
0.04
0.03
0
10
20
30
40
50
DBH (cm)


Subalpine fir
Whitebark pine
DBH (cm)
Age (years)
0
10
20
30
40
50
60
0
50
100
150
200
250

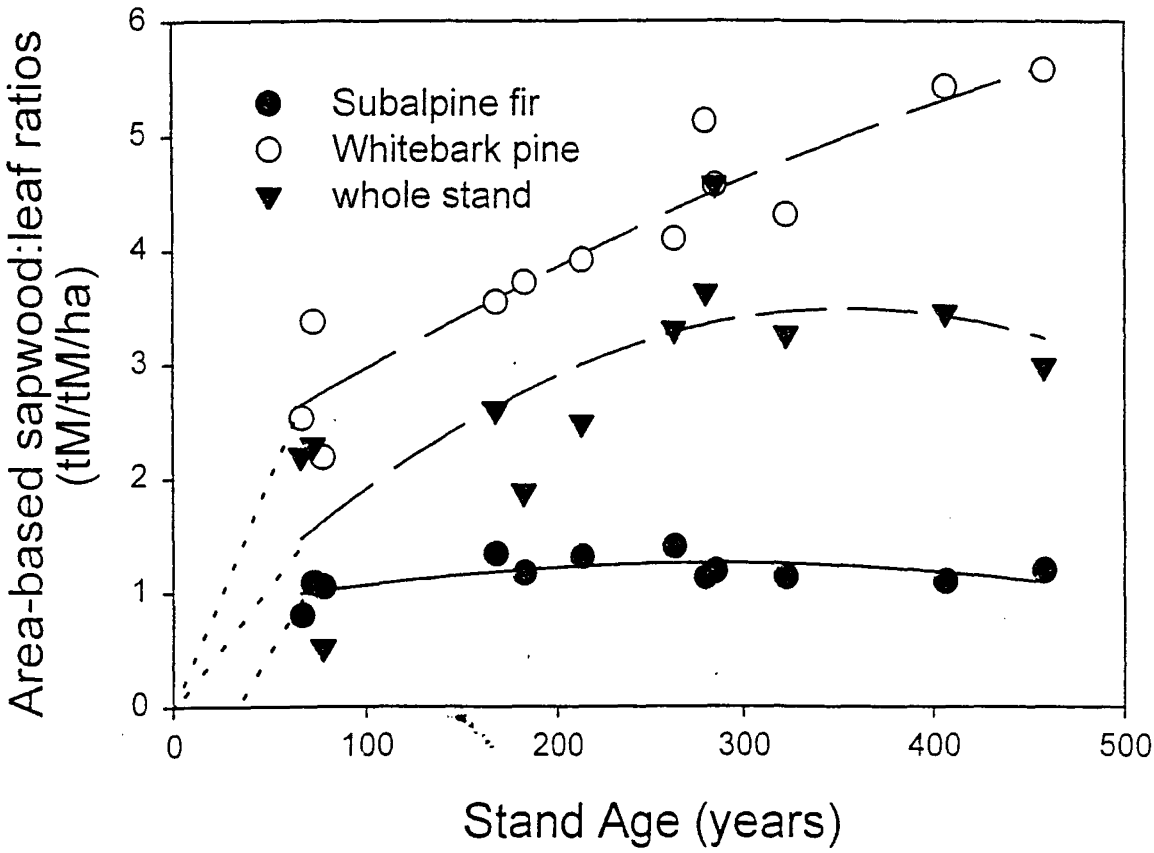

Area-based sapwood:leaf ratios (tM/tM/ha)
Stand Age (years)
Subalpine fir
Whitebark pine
whole stand
0
1
2
3
4
5
6
0
100
200
300
400
500

Fig. 8

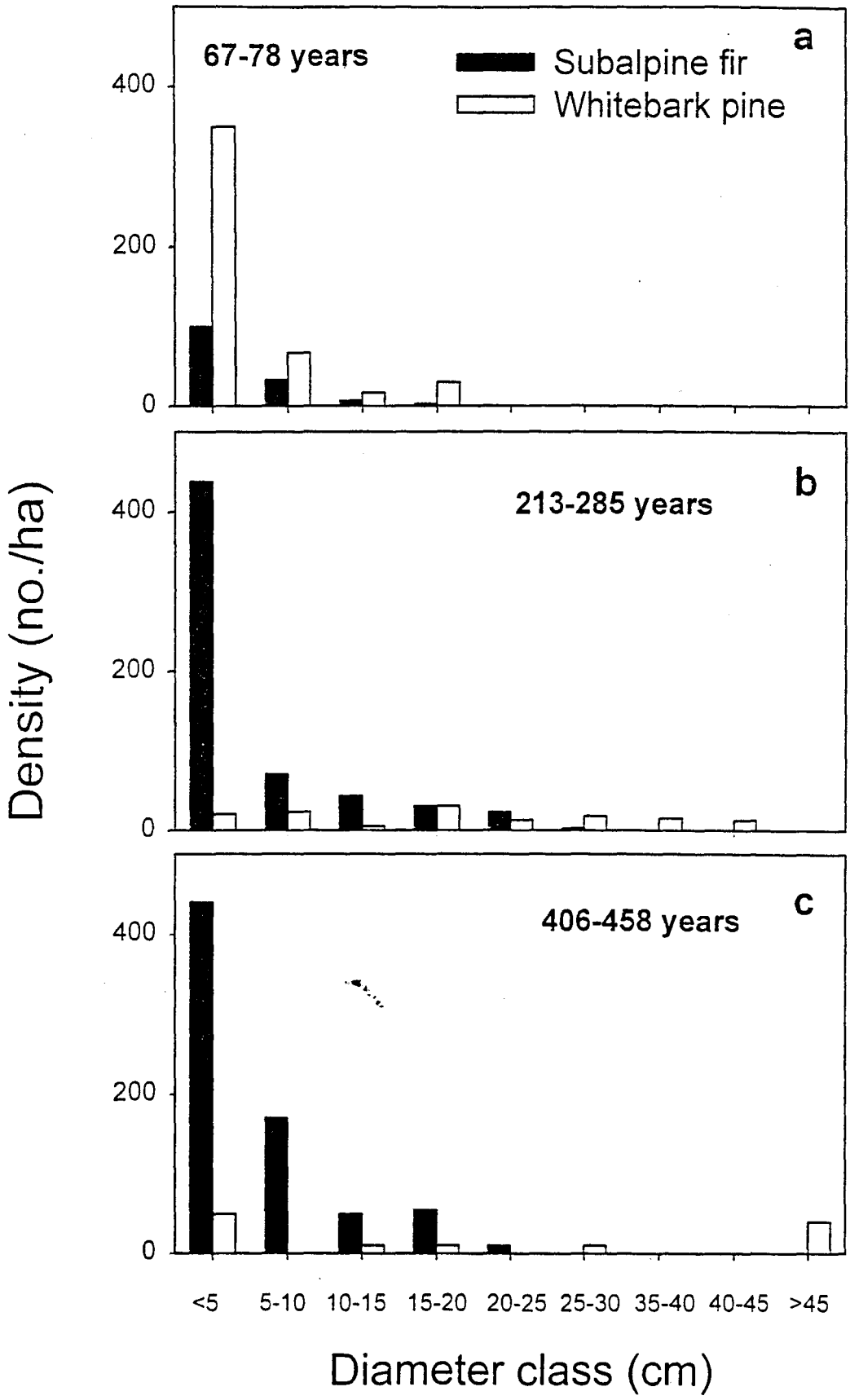

67-78 years
a
Subalpine fir
Whitebark pine
400
200
0
213-285 years
b
400
200
0
406-458 years
c
400
200
0
Density (no./ha)
<5
5-10
10-15
15-20
20-25
25-30
35-40
40-45
>45
Diameter class (cm)

Fig. 9

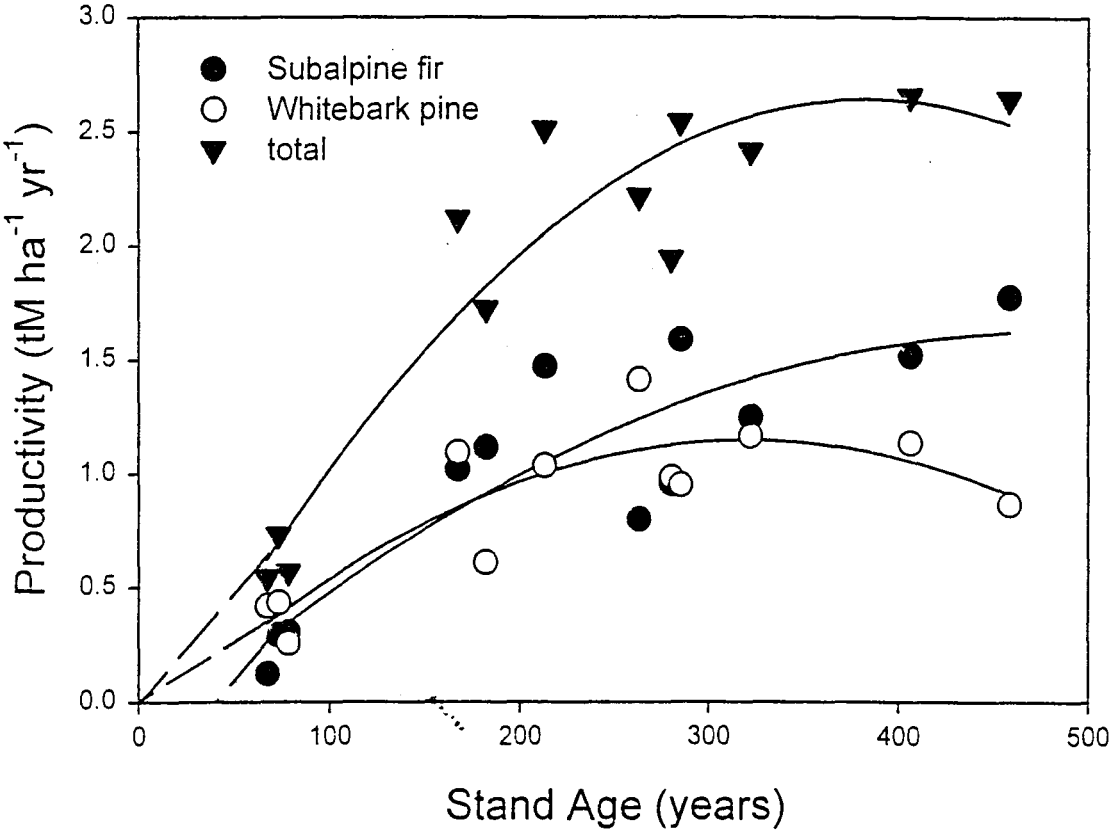

Subalpine fir
Whitebark pine
total
Productivity (tM ha-1 yr-1)
Stand Age (years)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
100
200
300
400
500

Fig 10

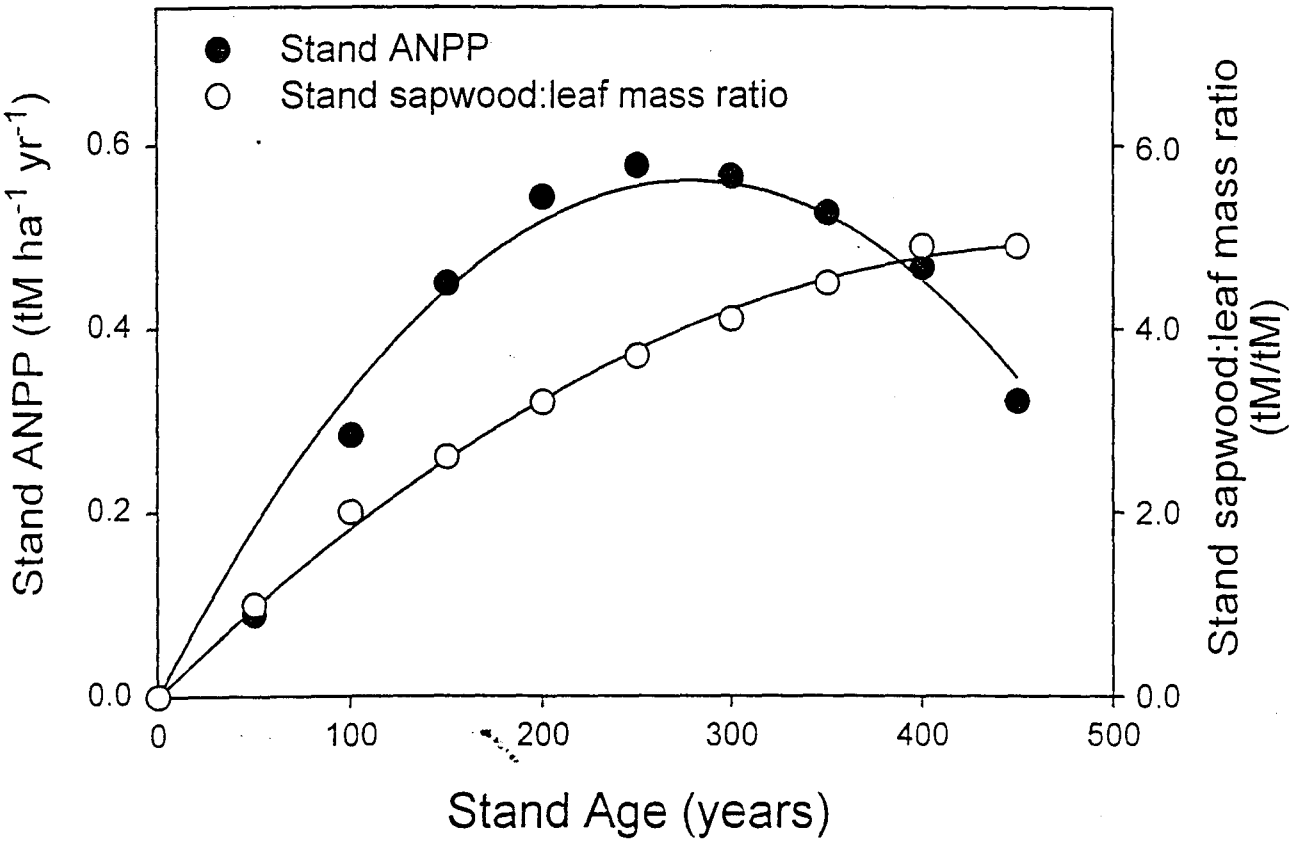

Stand ANPP
Stand sapwood:leaf mass ratio
Stand ANPP (tM ha-1 yr-1)
Stand sapwood:leaf mass ratio (tM/tM)
Stand Age (years)
0.0
0.2
0.4
0.6
2.0
4.0
6.0
0
100
200
300
400
500

Fig. 11

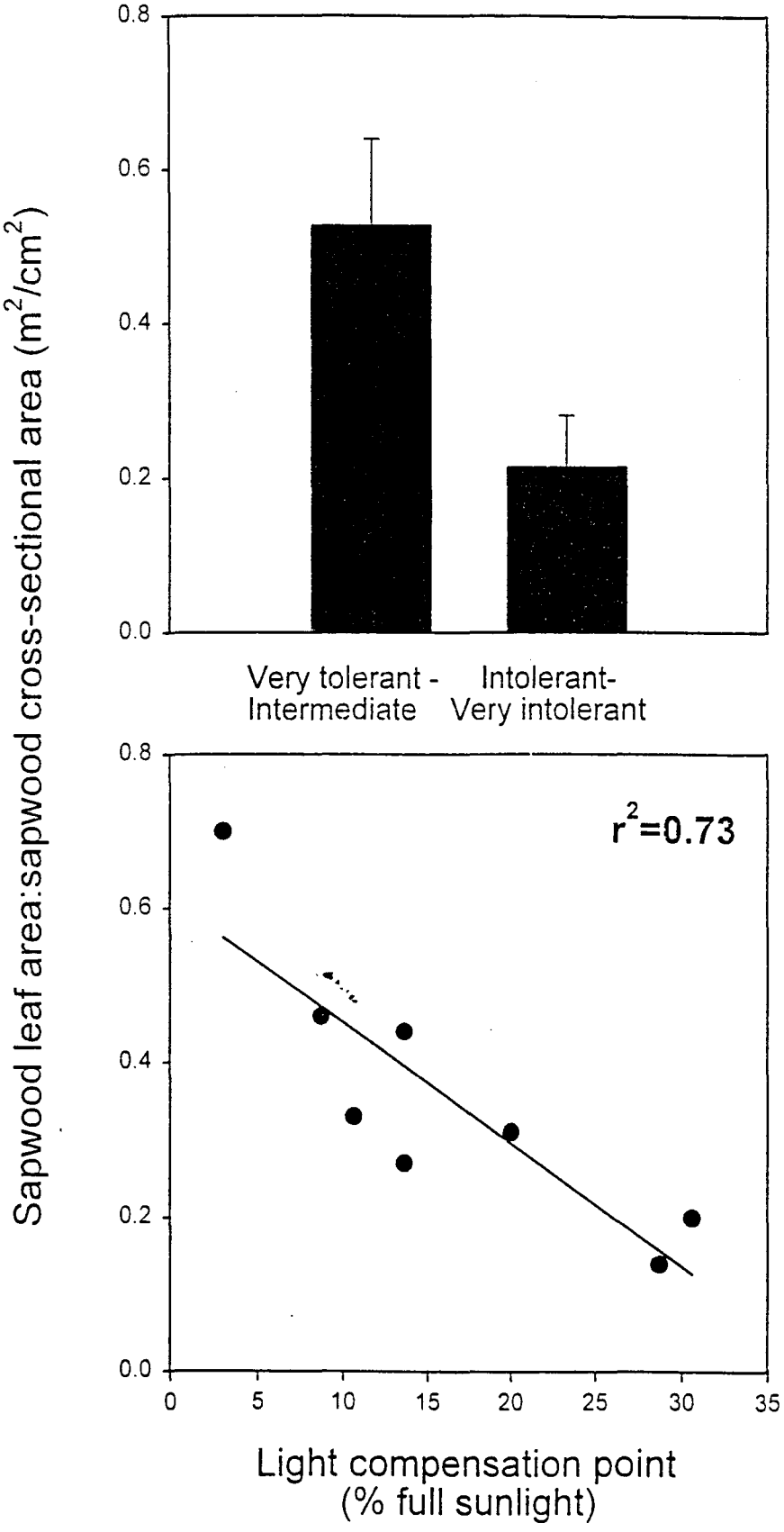

Sapwood leaf area:sapwood cross-sectional area (m^2/cm^2)
0.8
0.6
0.4
0.2
0.0
Very tolerant - Intermediate
Intolerant- Very intolerant
r^2=0.73
0
5
10
15
20
25
30
35
Light compensation point (% full sunlight)

Fig 12

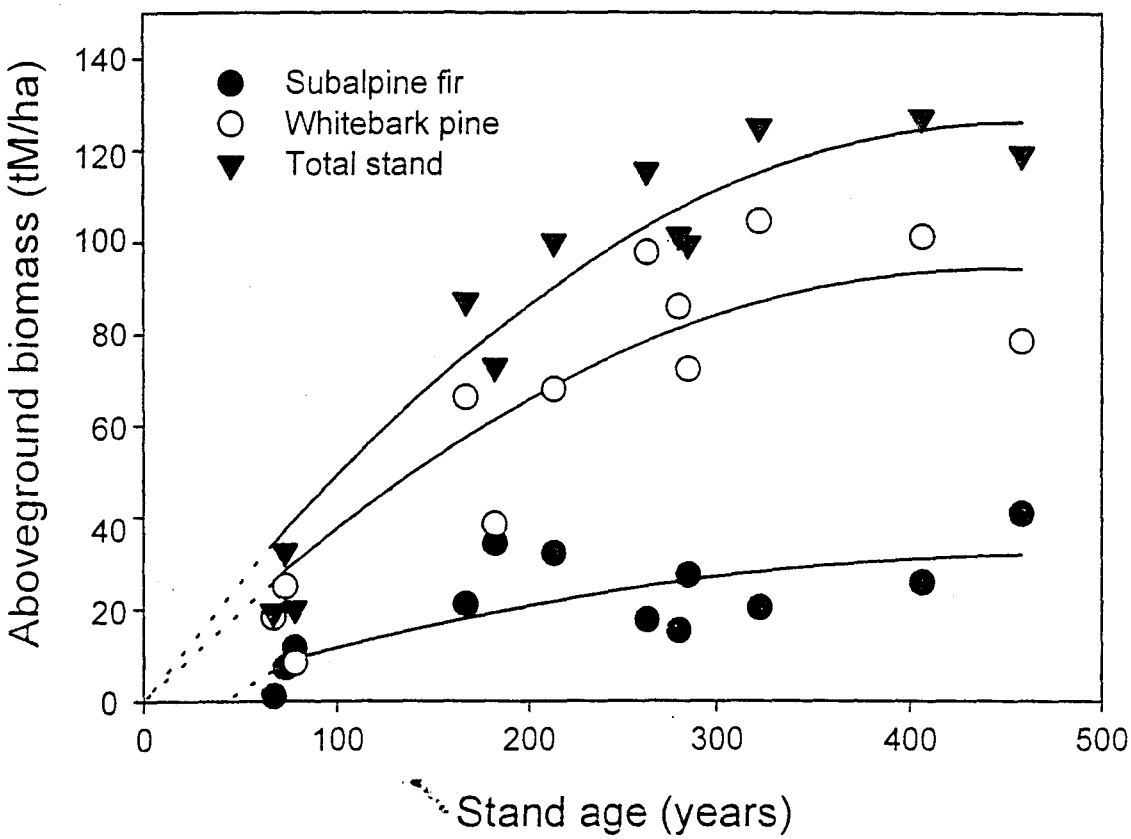

Aboveground biomass (tM/ha)
140
120
100
80
60
40
20
0
Subalpine fir
Whitebark pine
Total stand
0
100
200
300
400
500
Stand age (years)

Fig. 13

JUL 17 1998

Are old forests underestimated as global carbon sinks?

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Abstract

Old forests are important carbon pools, but are thought to be insignificant as current atmospheric carbon sinks. This perception is based on the assumption that changes in productivity with age in complex, multi-aged, multi-species natural forests can be modeled simply as scaled-up versions of individual trees or even-aged stands. We tested this assumption by measuring the net primary productivity (NPP) of natural subalpine forests in the Northern Rocky Mountains, and found that NPP ranges from 50% to 100% higher than predicted by a model of an even-age forest composed of a single species. If process-based terrestrial carbon models underestimate NPP by 50% in just one quarter of the temperate coniferous forests throughout the world, then global NPP is being underestimated by 145 Tg of carbon annually. This is equivalent to 4.3-7.6% of the missing atmospheric carbon sink. Our results emphasize the need to incorporate multiple-aged, species-diverse, mature forests into models of terrestrial carbon dynamics to approximate the global carbon budget.

Forested areas, particularly in the Northern Hemisphere, have been proposed as possible sinks of atmospheric carbon that are currently not accounted for by global carbon cycle models (1- 4). Several factors have been hypothesized to contribute to this missing carbon sink, including increased productivity by forests due to nitrogen deposition and greater atmospheric CO_2 concentrations, interannual climate variability (favoring either increased photosynthesis or decreased respiration), longer growing seasons, and regrowth of forests harvested in the early and middle parts of the 20^{th} century (2, 5-7). While young and recovering forests have obvious potential as carbon sinks, carbon exchange between old forests and the atmosphere is thought to be at equilibrium. We use the vague term "old forest" intentionally because, with the exception of canopy gap models, specific forest ages are rarely incorporated into either conceptual or process-based forest growth models (8). However, forests older than approximately 100 years are generally considered to be insignificant carbon sinks (6, 9).

The perception that old forests are not carbon sinks is based on two simple but interconnected assumptions about how forests grow: (1) age-related growth trends of individual trees and even-aged, monospecific stands can be extended to natural forests, and (2) respiration of tree stems and branches in old forests uses so much photosynthate that these forests can no longer accumulate carbon as biomass.

These assumptions are fundamental components of the simple conceptual model for forest growth, biomass allocation, assimilation, and respiration proposed by Kira and Shidei (10) in the late 1960's and further popularized by Odum (11, 12). The basic premise of the model is that as forests age, the decrease in biomass of photosynthetic leaves relative to respiring sapwood forces an inevitable decline in NPP (Figure 1).

Ultimately, it is assumed, "old" or "mature" forests reach a steady state with respect to carbon cycling (i.e., photosynthetic gross primary productivity, GPP, is equal to autotrophic respiration) and they sequester little, if any, atmospheric carbon (6, 9). These assumptions are also inherent in many process-based models of forest growth (13), and they are reinforced by widely accepted theory that basic biogeochemical cycles are conservative properties of ecosystems that do not vary much over a wide variety of species mixtures (8, 14).

We examined the validity of the first assumption (that even-aged stands can predict NPP of natural forests) by measuring growth rates, sapwood:leaf ratios, and biomass accumulation in natural, but structurally simple, subalpine forests in the northern Rocky Mountains that range in age from 67-458 years (15). These stands are dominated by two species, *Pinus albicaulis* (whitebark pine) and *Abies lasiocarpa* (subalpine fir) with the former dominating early-successional stands and the latter dominating late-successional stands. We compared biomass allocation, aboveground net primary productivity (ANPP), and total aboveground biomass in these forests to that modeled for simple, even-aged stands composed of 100% whitebark pine (16).

We found that sapwood:leaf mass ratios of modeled even-aged stands steadily increase with age as described by other simple forest-growth models (Figure 2A). In contrast, sapwood:leaf mass ratios of the natural forests diverge from those predicted from modeled stands at approximately 175 years and remain 25-50% lower for the next 300 years. This difference is due to continuous recruitment of both species in natural stands of all ages and the disproportional increase in the abundance of late-successional subalpine fir which has much lower sapwood:leaf ratios for trees of all ages.

Differences in ANPP are even more striking (Figure 2B). As described for other even-aged stands, ANPP of modeled stands reaches its maximum at approximately 250 years and decreases thereafter. ANPP in 200 year-old natural stands is almost twice that in modeled stands, and the difference between natural and modeled stands steadily increases throughout our sampled age range. Differences in stand aboveground biomass range from approximately 30% at 200 years to over 40% at 400 years (Figure 2C). These results indicate that long-term recruitment and late-successional species may have significant effects on stand productivity and that growth and carbon acquisition in old natural forests cannot be extrapolated from the productivity of even-aged stands. The patterns in NPP and biomass in these whitebark pine and subalpine fir stands can be generalized to other coniferous forests where changes in biomass allocation from early to late successional species result in much lower sapwood:leaf area ratios in mixed stands than in single species stands. Although whitebark pine and subalpine fir forests cover only 8-14% of the landscape in the Northern Rocky Mountains, the successional processes and the sapwood:leaf area dynamics in these two species are similar in boreal and temperate coniferous forests worldwide (17).

The second assumption (that high respiration costs of sapwood in old forests preclude carbon allocation to growth) is a fundamental component of basic forestry theory and process-based forest growth models. In these models respiration per unit sapwood remains constant as forests age and sapwood respiration is calculated as an exponential function of temperature and biomass, irrespective of tree size or age, using the equation: $R = aBQ^{(T)}$, where: a is a constant, B is biomass, Q is the temperature coefficient of respiration and T is sapwood temperature (13, 18). This calculation results

in modeled forests reaching a steady state in carbon exchange in less than 100 years. In nature, however, neither trees nor forests show constant respiration rates per unit of sapwood or biomass over time (19, 20). Instead, stem respiration decreases with increasing tree size (21, 22). By not including size- or age-dependent decreases in stem maintenance respiration per unit sapwood volume in process-based models of forest growth, respiration in older stands can be overestimated by a factor of 2-5 (estimated from 22), and thereby provide an intuitively satisfying, but misleading, mechanism for the first assumption (23). In contrast, the fact that stem respiration decreases with tree size provides a potential mechanistic explanation for the lack of growth decline that we found in old subalpine forests. The omission of size- and age-related decline in stem respiration from models of forest productivity could potentially explain why estimates of low net primary productivity in mature stands have been attributed to increasing woody tissue respiration (11).

Alternative hypotheses have been proposed to explain reduced productivity as forests age. These include declines in nutrient availability and hydraulic conductivity (thereby reducing photosynthesis) (20, 24). Although these alternative hypotheses for the cause of forest growth decline suggest allocational or physiological mechanisms to explain why growth of individuals or stands decline through time, they do not address the effects that succession and species diversity may have on maintaining long-term productivity and biomass accumulation in natural forests.

To estimate the potential of older forests as carbon sinks, we calculated the increase in carbon uptake if annual NPP of temperate coniferous forests [4.65 Mg ha^{-1} yr^{-1} (25, 26)] was underestimated by up to 100%. This range of growth reduction

is based on our results in subalpine forests in the Northern Rockies (Figure 2), and was applied to 25% of temperate coniferous forests globally [i.e., 62.5×10^6 ha of ~250×10^6 ha, (27)]. Assuming a conservative estimate of growth reduction of 50% and that 1.9-3.4 Pg of C is still missing to balance the global carbon budget in global climate models (1, 2, 4), then 4.3-7.6% could be from growth of older temperate coniferous forests (Figure 3). If we refine this analysis to include only the 137.6×10^6 ha of protected forests in Europe, USSR, and North America that are coniferous (28), then 5.5-10% of the global carbon sink may be accounted for (Figure 3). Although we do not know the past use of these protected areas, they provide a conservative estimate of the current area occupied by older, natural stands of mixed-species.

With respect to the two fundamental assumptions for forest productivity, we found that: (1) if we account for recruitment and succession, growth declines in old forests may be less in magnitude and occur over much longer periods of time than previously predicted from measurements of individual trees and even-aged, single-species stands, and (2) respiration rates in old forests decrease with tree and stand age, and do not provide a clear mechanism for explaining declines in forest growth. Forests cover ~28% of earth's land surface [~4.1 billion hectares, (29)] and account for a large proportion of the global terrestrial carbon budget (5, 30). Because of forests' considerable contribution to global net primary productivity [>60%, (25, 30)], it is crucial to incorporate basic ecological principles and realistic rates of carbon exchange into models of terrestrial carbon budgets. Our results also suggest that species composition and diversity matter to ecosystem properties in old forests, and that some basic biogeochemical processes in forests may not be as conservative as previously thought.

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15. Trees of each species were selected to represent their typical ranges of diameters at 140 cm above ground (dbh) and cut down at the base. Total tree height and the basal diameter of all live branches were measured on each bole. Three to 5 cm thick disks were cut at 2-m intervals from each bole and cross-sectional areas of sapwood, heartwood, and bark on each disk were traced on clear acetate. The volume (in cubic meters) of each component in each 2-m bole section was calculated using the areas of the disks at each end of the sections in the following equation: volume = $((A_1 + A_2)/2) \times 2$ m, where A_1 = initial area in square meters and A_2 = terminal area in square meters. Bole volume was calculated by summing all sections for each tree. Volume of each component was converted to mass using the specific gravity (in kilograms per cubic meter) of the heartwood, sapwood, and bark. A subsample of branches from all trees of each species were used to calculate the regression relationship of leaf mass and sapwood mass to branch diameter and these regressions were used to calculate the leaf mass and branch sapwood mass for each tree.

We measured the width of the five most recent annual rings (1991-1995) for all 23 trees at 3 different places on each disk section. This width was subtracted from all disk sections and bole biomass was recalculated using the 5-year pre-harvest estimates of tree size. The 5-year pre-harvest mass was subtracted from current bole mass for each tree and divided by 5 to estimate current annual aboveground bole productivity. The annual productivity of the bole, as a percentage of current bole mass, was used to

estimate branch productivity. Leaves from ten randomly chosen branches from different trees for each species were separated into the sample year's current growth, and that of all previous years, prior to drying and weighing. From this we developed estimates of the proportion of total leaf mass that was a single year's production. This ratio was applied to the canopies of all trees to estimate an annual rate of leaf productivity for each species. Bole, branch, and leaf productivity were summed as an estimate of total aboveground productivity (ANPP) for each species by dbh.

We constructed biomass allocation and ANPP estimates for forests using empirical data from 12 natural stands in the Bob Marshall Wilderness in Montana, 300-400 km north of the harvest site. These stands varied in age from 67 to 458 years old, and appeared to have regenerated after stand-replacing fires. In each stand, 400 m^2 circular plots were located and all tree stems were classified into 5 cm size classes. In each plot 10-20 trees of various sizes, but including the largest trees, were cored as close to the ground as possible and aged by adding the age at the height of the core to regression estimates for the number of years the tree took to reach core height. Over 95% of the basal area in these stands was whitebark pine and subalpine fir. We entered the median dbh for each dbh class (e.g., 7.5 in the 5-10 cm class) into the regression models that were developed using the harvested whitebark pine and subalpine fir to calculate sapwood mass, leaf mass, and ANPP. Sapwood mass, leaf mass, and ANPP of all dbh classes were summed for each plot and scaled to tM/ha. Time-based models were built using the age of the oldest cored tree in each stand for stand age.

16. To provide a simple null model for stands without subalpine fir and without recruitment over time, we used the biomass allocation and productivity regressions from

harvested whitebark pines to model biomass allocation and productivity of a theoretical, even-aged, whitebark pine stand. This stand began with 800 3.8 cm dbh stems/ha at 50 years (this estimate was reached by doubling the number of whitebark pines in this size class in the two youngest natural stands that were 70-80 years old), experienced 30% mortality every 50 years, and had all surviving trees grow into the next largest age class every 50 years. These inputs were designed so that modeled stands at 450 years in age had similar tree densities in the >50 cm dbh classes to our natural stands that exceeded 400 years in age. Such consistent mortality may be unrealistic for many natural stands, but it is representative of a much larger data set on stand dynamics in the Bob Marshall Wilderness (R. E. Keane, S.F. Arno. *West J. Appl. For.* **8**, 44-47 (1993).

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28. Additional productivity of protected forests is based on areal estimates given in: World Resources Institute, *World Resources 1986* (Basic Books, New York, 1986). Protected forest areas are: 22.3×10^6 ha in Europe, 36.1×10^6 ha in North America, and 158×10^6 ha in the former USSR. Coniferous forest as a percentage of total forest area in each region is: 50% in Europe, 44% in North America, and 70% in the former USSR. The estimate of average NPP used in calculations for protected European and North American forests was 4.65 Mg ha^{-1} yr^{-1} (temperate coniferous forest), and for forests in the former USSR was 2.38 Mg ha^{-1} yr^{-1} (boreal forest), from (22).

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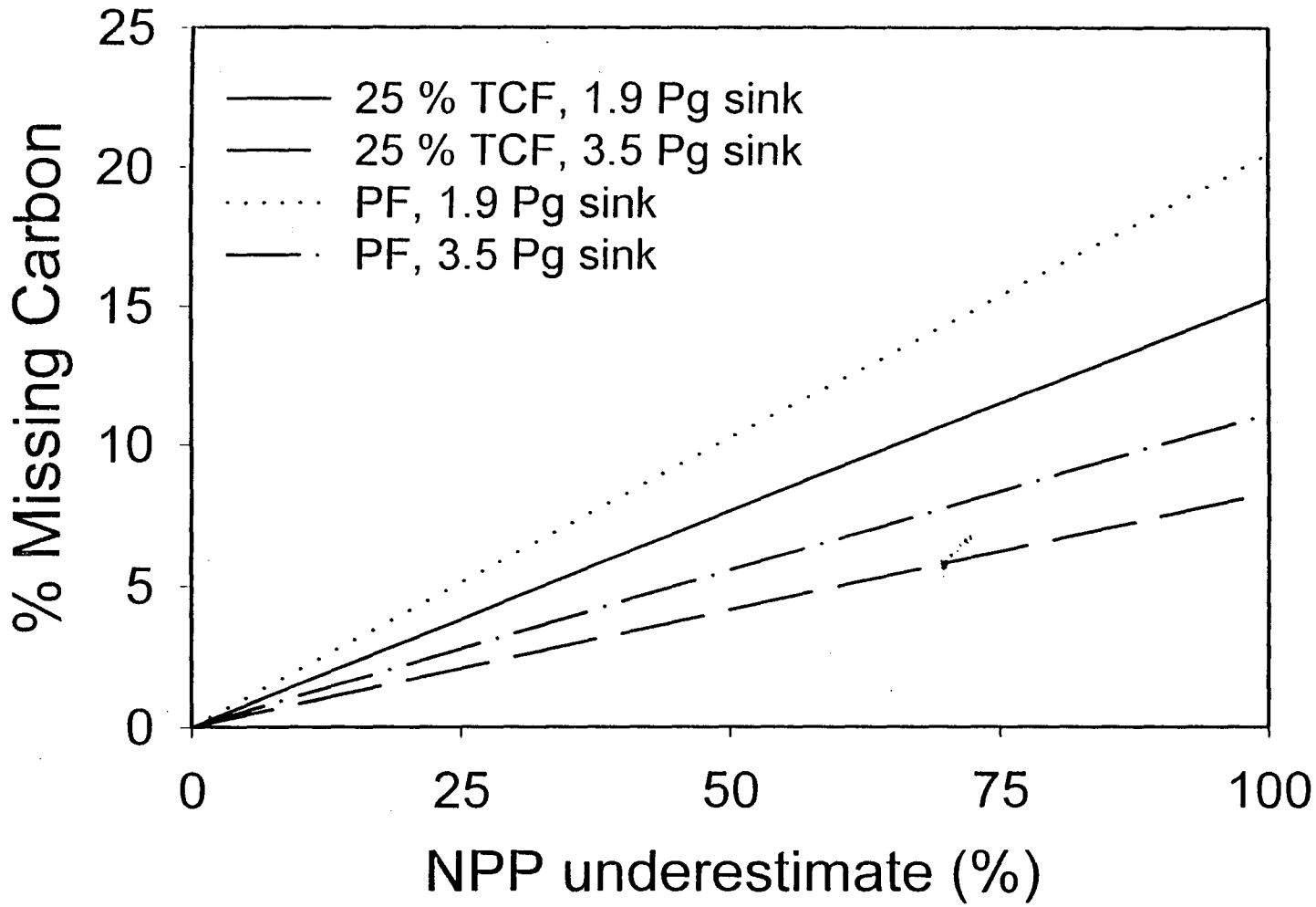
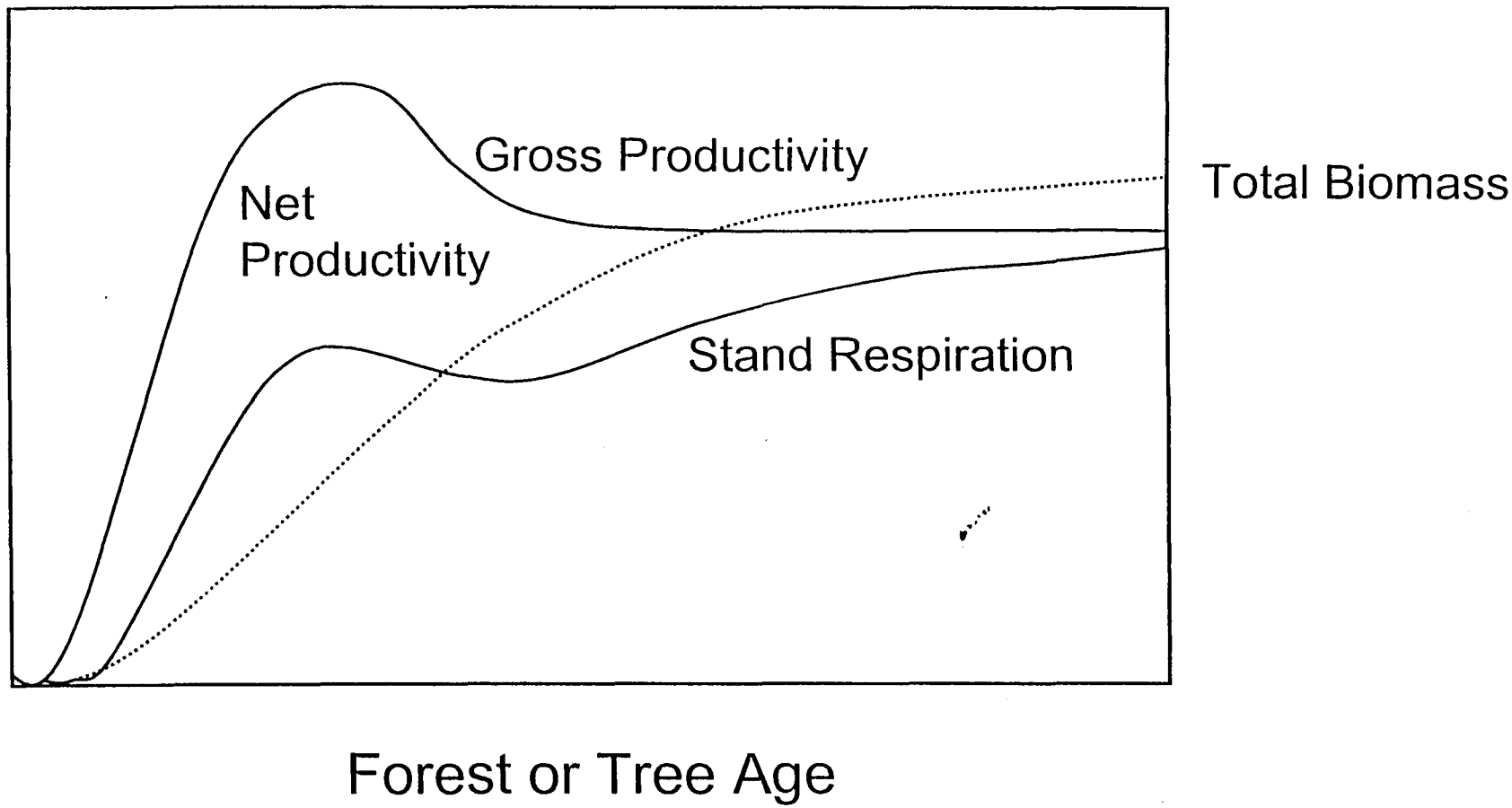
Figure legends:

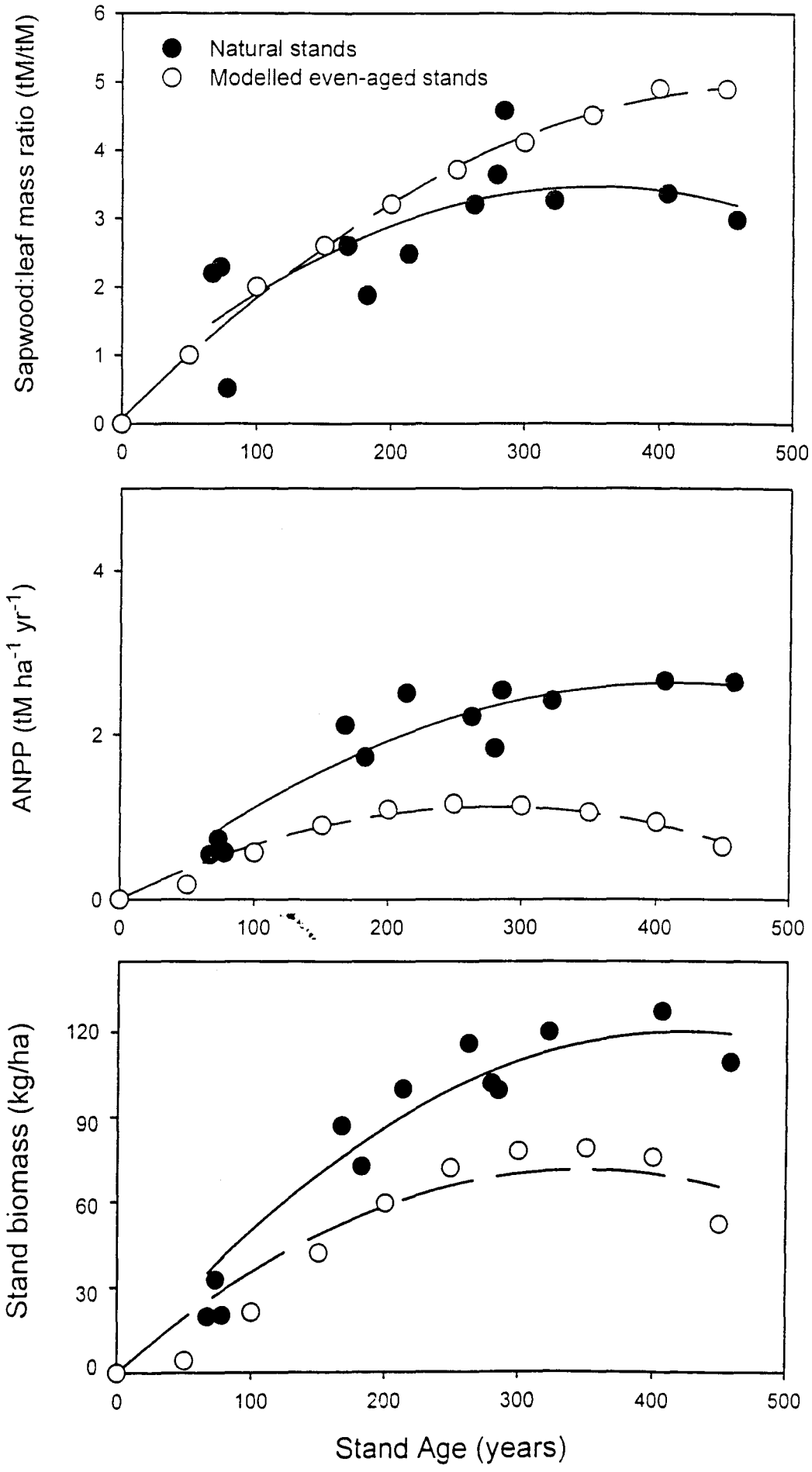
Figure 1: Gross primary productivity (GPP), stand biomass, and stand respiration as a function of increasing forest or tree age. The difference between GPP and stand respiration is net primary productivity (NPP). Redrawn from (10, 11).

Figure 2: Whole-stand sapwood:leaf mass ratios (A), annual net primary productivity (B), and biomass (C) for natural subalpine forest stands of different ages in the northern Rocky mountains and simulated whitebark pine stands composed of even-aged stands of whitebark pine without recruitment over time.

Figure 3: Percentage of missing carbon sink accounted for if models of forest growth underestimate NPP of coniferous forests in the Northern Hemisphere. Lines illustrate amount of missing carbon accounted for if NPP is underestimated for 25% of temperate coniferous forests (TCF) or for all protected forests (PF) in Europe, North America and the former Soviet Union (25). Values are expressed as percentages of high (3.5 Pg yr^{-1}) and low (1.9 Pg yr^{-1}) estimates of missing carbon.


25 % TCF, 1.9 Pg sink
25 % TCF, 3.5 Pg sink
PF, 1.9 Pg sink
PF, 3.5 Pg sink
% Missing Carbon
0
5
10
15
20
25
0
25
50
75
100
NPP underestimate (%)


Gross Productivity
Net
Productivity
Stand Respiration
Total Biomass
Forest or Tree Age


Natural stands
Modelled even-aged stands
Sapwood:leaf mass ratio (tM/tM)
ANPP (tM ha-1 yr-1)
Stand biomass (kg/ha)
Stand Age (years)
0
100
200
300
400
500
1
2
3
4
5
6
30
60
90
120

POOR QUALITY

The following pages are scanned at the best possible quality setting. The original pages are of poor quality and this is the best possible reproduction.

Water use by whitebark pine and subalpine fir: Stand water use during succession and implications of fire suppression.

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Key Words: Forest Water use, succession, Pinus albicaulis, Abies lasiocarpa, fire suppression, sap flow.

Abstract

As early successional species in temperate coniferous forests are gradually replaced by late successional species significant changes in forest carbon, water and nitrogen cycles may occur. It has been shown that shade tolerant, late successional species exhibit low sapwood to leaf area ratios relative to early successional, shade intolerant species. A direct consequence of the increase of leaf to sapwood area ratio in late successional species is a potential increase in stand leaf area index and stand water consumption as succession proceeds. In subalpine forests of the interior northwest, fire suppression has contributed to dramatic shifts from shade intolerant, early successional whitebark pine to shade tolerant, late successional subalpine fir. The hydrological consequences of this replacement at the stand-, watershed- or regional- level have not been assessed. We used sap flow techniques to compare water use between whitebark pine and subalpine fir of different sizes in western Montana and extrapolated the relationships between water use and tree size to known size classes of trees in natural forests ranging from 67 to 458 years old. Whitebark pine exhibited higher rates of leaf gas exchange and leaf area related sap flow than subalpine fir. However, much higher allocation to foliage in subalpine fir compensated for low leaf level rates of water use, and sapwood related sap flow was higher in subalpine fir. We found evidence of hydraulic limitations in older whitebark pines but not in subalpine firs. A strong relationship between tree size and cumulative daily tree water use in both species allowed us to estimate stand-level water use in 12 natural stands in western Montana dominated by whitebark pine and subalpine fir, ranging from 67 to 458 years old. Results showed that incursion of subalpine fir into whitebark pine stands may increase stand water use up

to 100%. This increase is largely due to the increase in leaf area index, although a smaller, but significant, fraction results from species-specific differences in water use (i.e. higher water use in subalpine fir due to its high allocation to foliage).

Introduction

As early successional species in temperate coniferous forests are gradually replaced by late successional species significant changes in forest carbon, water and nitrogen cycles may occur (Waring and Running 1998; Landsber and Gower 1997). Biomass allocation data for coniferous species of the Northwestern U.S. (Margolis et al. 1995; Callaway et al. 1994; Waring and Running 1998) combined with successional trends summarizes by Pfister et al. (1977) indicate that late successional species exhibit low sapwood to leaf area ratios (cross section sapwood area at breast height to total tree projected leaf area) relative to early successional species (Callaway et al. submitted). These functional attributes at the species level may significantly contribute to whole stand productivity in older forests as succession proceeds and early successional, shade intolerant species are replaced by late successional, shade tolerant species with lower ratios of non-photosynthetic to photosynthetic tissues (lower above-ground respiration costs; Callaway et al. submitted). A direct consequence of the increase of the leaf to sapwood area ratio in late successional species is a potential increase in stand leaf area index and stand water consumption. LAI increases in late successional stands will only occur if 1) sapwood basal area of the later successional species is maintained similar to that of the early successional species replaced, or 2) if decreases of sapwood area of the later successional species do not compensate for the increase in leaf to sapwood area ratio. The degree to which changes in stand LAI (which in natural stands result from successional species replacement) translate into changes in stand water use, depends on species-specific stomatal control of water use (i.e. differences between early and late

successional species) and on the degree to which water loss of the dominant species is controlled by stomata or by the boundary layer (Jarvis and McNaughton, 1986). While Pinus species, which in the northern Rockies tend to be early successional (Pfister et al. 1977), exhibit a strong stomatal control of transpiration (Loustau et al. 1996), dense needle packing and compacted canopy structure in late succesional species (e.g. firs) result in self-shading, increased boundary layer, relative decoupling of stomata from external environmental conditions, and potential reductions in water loss. Therefore, stands of early successional species of a given LAI may use more water compared to stands of late successional species with the same LAI. However, much higher LAI in late successional stands (due to high biomass allocation to leaves in late successional species) might compensate for reductions of water loss at the leaf and tree level and result in high water use at the stand level. Thus, the degree to which successional species replacement alters stand water cycles, depends on the complex interaction between species-specific functional (stomatal control of water loss) and structural attributes (canopy structure, biomass allocation) and the proportion of each species as succession proceeds.

With the advent of new techniques, numerous studies have examined environmental controls of stand-level water loss in conifer species (e.g. Schiller and Cohen 1995; Loustau et al. 96; Granier and Loustau 1994; Čermák et al. 1995; Arneth et al. 1996; Cienciala et al. 1994; Hatton and Vertessy 1990; Cienciala et al. 1998). However, to our knowledge no study has addressed potential changes in stand-level water use as forests age and successional species replacement occurs. Conifer forest productivity is thought to decrease as forests age (Ryan et al. 1997; but see Callaway et al. submitted). Contrary to what was previously thought (see Waring and Running 1998),

this decline cannot be attributed to increases in respiratory losses (see Ryan et al. 1997 for a review) and several alternative hypotheses have been proposed. For instance Ryan and Yoder (1997) suggested that hydraulic limitations on photosynthesis and the amount of LAI that can be supported are sufficient to account for the decline in forest productivity. Consistent with this hypothesis, Mencuccini and Grace (1996) found that hydraulic resistance of monospecific, even aged Pinus sylvestris stands increase with stand age. The extent to which older stands experience hydraulic limitations depends not only on the structural properties of individual trees as they age, but on potential changes in stand water use and soil water resources as successional species replacement occurs.

Fire exclusion policies implemented during the past 60-80 years in western forests have resulted in large-scale successional changes in conifer forests throughout North America (Arno 1980). In subalpine forests of the interior northwest, fire suppression, beetle epidemics, and introduced pathogens have contributed to dramatic shifts from shade intolerant, early successional whitebark pine (Pinus albicaulis Engelm.) to shade tolerent, late successional subalpine fir (Abies lasiocarpa (hook.) Nutt.) (Arno and Petersen 1983, Keane et al. 1990, Keane and Arno 1993). The result is that whitebark pine, which once dominated about 50% of the subalpine forests in Montana, has been largely replaced by subalpine fir and now occupies only a fraction of its former range (Keane and Arno 1993). The hydrological consequences of this replacement at the stand-, watershed- or regional- level have never been assessed. We used sap flow techniques to compare water use between whitebark pines and subalpine firs of different sizes in western Montana and extrapolated the relationships between water use and tree size to known size classes of trees in natural forests ranging from 67 to 458 years old. Our

objectives were to investigate the relative effect of species replacement and changes in stand structure (sapwood area and leaf area index) on stand water use during succession.

Site

The study site was located in a subalpine forest at 2300 m elevation in the Sapphire Mountains of the Northern Rockies (46° 05'N; 114° 50' W) approximately 90 km south of Missoula, Montana, USA. The site, of approximately 5 ha, is on a southwest-facing slope of 10-15% with a granitic substrate. The site was subjected to partial cutting of the overstorey trees in the early 1960's, although basal area was similar to that found in natural stands of similar age (35 m^2 ha^{-1}). Mean annual precipitation and temperatures for July and January for this habitat type (*Abies lasiocarpa-Luzula hitchcockii*) are 720 mm, 14 °C and -10 °C, respectively (Pfister et al. 1977). Field sampling was conducted from July 10 to July 15, 1996, approximately three weeks after snowmelt. The weather was clear with mean temperatures of 12.7 °C.

Methods

Twenty trees of subalpine fir and whitebark pine of diameters ranging from 2.5 to 45 cm (at 1.3 m, DBH) were sampled for leaf-level measurements of gas exchange and xylem water potential and tree-level water use. For consistency and to maintain conditions similar to those in natural stands we sampled trees that were in closed stands, but with canopies that were not in contact with neighbors. None of the trees sampled were infected by blister rust.

Xylem water Potential and gas exchange

Xylem water potential at predawn was measured on terminal twigs sampled at the middle portion of the crown for each of the 20 trees of each species on July 13th. Subsequent measurements during the day were taken concurrent with gas exchange measurements from 4 trees of each species representing the full range of DBH. Water potential was measured with a Scholander-type pressure bomb (PMS, Oregon, USA). Photosynthesis rates and stomatal conductance were measured on fully illuminated mature needles (sampled at the lower canopy) at periodical intervals during the day with a portable photosynthesis system (LI-COR 6200, Licor Inc. Nebraska, USA). Transpiration rates were calculated from stomatal conductance and leaf to air vapor pressure difference, which in turn was calculated from measurements of air vapor pressure and leaf temperature taken with the cuvette open. Needles were brought to the laboratory and total projected area was measured with an image analysis system (Mocha, Jandel Scientific). Gas exchange rates were than corrected for actual leaf area in the cuvette.

Foliar $^{13}C/^{12}C$ ratio and total N content

Foliar stable carbon isotope ratios were used as indicators of long-term water use efficiency (Farquhar and Richards 1984; Ehleringer and Osmond 1989). Because both species were sampled at the same site, potential effects of varying evaporative demand on water use efficiency (Marshall and Zhang 1994) were not a concern. Oven-dried mature leaves from each tree were coarsely ground to homogenize the leaf tissue. A sub-sample from each branch was finely ground (60 mesh) for stable carbon isotope and total

nitrogen content (% dry weight) analysis. Samples were analyzed at the Stable Isotope Laboratory of the Institute of Ecology (University of Georgia). Carbon isotope ratio was expressed relative to PDB (PeeDee Belemnite).

Tree water use

Sap flow was measured on 10 subalpine fir and 10 whitebark pine trees encompassing the full DBH range on July 12th and on 10 additional trees per species on July 14th. Sap flow use was measured using the heat pulse method, which uses pulses of heat as markers in the sap stream (Jones et al. 1988). Probe lengths (Thermalogic, Pullman, Washington) varied from 20 mm (inserted in the smallest trees) to 35 mm long (inserted in the larger trees). The principles and calculations of heat pulse velocity, sap velocity and total tree sap flow (Q) are described in Cohen et al. (1981) and Schiller and Cohen (1995). Zero sap flow conditions were assumed to occur at dawn. The volumetric specific heat of wet wood was determined gravimetrically (Campbell et al. 1991) from sapwood samples taken in 9 trees of each species. There were no differences between small, medium and large trees and an average value was used per species. Wounding was negligible and no wounding correction was made. Sap flow per tree was calculated from the sap flow velocity and the sapwood area using the weighted average method (Hatton et al. 1990). CR10 and 21X data loggers (Campbell Scientific, Logan, Utah) were used to control the relays operating the heaters and record the data. Only one probe was inserted per tree at 1.4 m on the northeast side. Once installed, probes were insulated with 6 cm thick foam and wrapped with padded reflective material. Fourteen whitebark pine and 9 subalpine fir of those sampled for sap flow were harvested to build regression models for

biomass allocation and growth (Callaway et al. submitted). In these harvested trees, total sapwood area was determined by staining 5 cm thick transverse disks taken at the probe insertion level (1.4 m) with bromecresol green (Kutscha and Sachs 1962). Stained cores taken at the probe insertion point and at the opposite side of the trunk were used to calculate sapwood area in non-harvested trees. Total tree leaf area in harvested trees was also determined as specified in Callaway et al. (submitted). Because of probe failure and probe insertion in non conducting sections of the sapwood, only 16 subalpine fir and 15 whitebark pine could be used to estimate water use.

Weather variables (relative humidity, air temperature, global radiation and wind velocity) where measured every minute and averaged every 30 min. in a nearby clearing concurrent with sap flow measurements. The driving force for transpiration (leaf to air vapor pressure difference as a mole fraction) was calculated from air temperature and relative humidity assuming that leaf temperature in these conifer needles approaches air temperature (Campbell 1977).

Stand-level water use

The regressions of DBH and total tree sap flow developed for each species in our study site were used to estimate stand-level water use in 12 natural stands ranging from 67 to 458 years old in the Bob Marshall Wilderness Complex in Montana (BMWC). Whitebark pine has the potential to dominate 35-40% of the subalpine landscape within the BMWC (Bain 1990). However, blister rust epidemics and successional replacement by subalpine due to fire exclusion policies during the past 60 years have resulted in a substantial whitebark pine decline and a gradual increase of subalpine fir (Keane et al.

1994). We minimized microclimate differences between our sap flow sampling site and the subalpine forests of the BMWC by selecting only those stands in the BMWC that were the same habitat type as our sap flow sampling site (*Abies lasiocarpa-Luzulahitchcockii*, Pfister et al. 1977). In each stand, 400 m^2 circular plots were located and all trees were classified into 5 cm size diameter classes. Stand age was determined by sampling 10-20 trees of varying sizes, and coring as close to the ground as possible. Tree age was corrected by adding regression estimates of the number of years it took to reach core height.

Stand water use was then estimated by adding the water use of trees in each size class, determined from the regressions of DBH and total tree sap flow and the total number of trees in each size class.

Statistical Analyses

Regression models of leaf carbon isotope ratio, nitrogen content, total tree sap flow (Q), sapwood- and leaf area- related sapflow (Qs and Ql, respectively) and tree size were statistically compared with species effects and slopes differences using general linear models (GLM) procedures (SAS). Statistically significant ($p< 0.05$) interaction DBH* species term was indicative of slope differences between species.

Results

Xylem water potential and leaf-level gas exchange

Approximately three weeks after snow melt predawn xylem water potential (Ψ_{pd}) of whitebark pine and subalpine fir was high and not significatly different (-0.88 ±0.04 s.e. and -0.64 ± 0.04 s.e. for whitebark pine and sulapine fir, respectively). During the day xylem water potential decreased moderately reaching a minimum of -1.49 ±0.02 s.e. in whitebark pine and -1.46 ±0.69 s.e. in subalpine fir.

Under clear sky conditions, gas exchange rates were generally higher in terminal, fully iluminated shoots of whitebark pine compared to subalpine fir (Figure 1). From early to mid-morning, photosynthesis rates were similar in both species but during mid-morning to mid-afternoon values were significantly higher in whitebark pine (maximum rates of 11 μmol CO_2 m^{-2} s^{-1}) than in subalpine fir (maximum rates of 6 μmol CO_2 m^{-2} s^{-1}; Figure 1a). Transpiration rates were higher in whitebark pine than in subalpine fir throughout the day (Figure 1b). Low transpiration rates in subalpine fir resulted in higher instantaneous water use efficiency, particularly early and late in the day (Figure 1c).

Photosynthesis rates in subalpine fir tended to saturate at ca. 6 μmol CO_2 m^{-2} s^{-1} between 500 and 750 μmol m^{-2} s^{-1} of photosynthetically photon flux density (PPFD), while whitebark pine did not exhibit a clear saturation point, reaching maximum values of 11 μmol CO_2 m^{-2} s^{-1} at ca. 1800 μmol m^{-2} s^{-1} of PPFD (Figure 2).

Carbon isotope ratios and leaf nitrogen content

Carbon isotope ratios of mature leaves of whitebark pine were significantly higher than in subalpine fir ($p < 0.05$; Table 1). Because the two species were sampled at the same site and evaporative demand was similar for both species, carbon isotope ratios are a good integrated measure of long-term WUE (Farquhar and Richards 1984; Ehleringer

and Osmond 1989). Thus, contrary to our instantaneous measurements taken under non water stress conditions, long-term WUE was higher in whitebarpine than in subalpine fir. Total nitrogen content (% dry weight) in leaves of both species was similar and consistent with values reported in the literature for coniferous species (Reich et al. 1997). Neither long-term WUE or %N varied significantly with tree size measured as the diameter at breast height (DBH; not shown).

Sap flow and tree water use

Radial patterns of sap velocity (i.e. changes in sap velocity with xylem depth) varied substantially, from similar velocities at different depths to strong declines from the outer (closest to the cambium) to the inner xylem (closest to the heartwood). Small, medium and large trees (with probe lengths ranging from 20 mm in small trees to 35 mm in large trees) exhibited similar patterns and all data for a single species were pooled. Overall, both species showed declines in sap velocity from the outermost to the inner portion of the xylem (Figure 3). However, this decline was significantly greater in whitebark pine (up to 60%) than in subalpine fir (up to 80%).

Diurnal variations in sap flow (in Kg h^{-1}) in whitebark pine and subalpine fir during clear July days closely followed changes in leaf to air vapor pressure difference (Figures 4 and 5) with maximum rates from noon to early afternoon and minimum (although significant) throughout the night. Absolute minimums were consistently observed at dawn (between 4 and 5 in the morning) when the zero flow assumption for our calculations was made (see methods). Night-time signals were consistently low and noisy (fluctuating randomly) suggesting that the method might loose accuracy under very

low sap flow velocities. Because of this uncertainty we refer here to total daily sap flow as the accumulated flow during day light hours only (from 5 a.m. to 10:30 p.m.). Maximum total tree sap flow rates varied from 0.5 Kg h^{-1} in small trees (DBH < 5 cm) to 7 Kg h^{-1} in large trees (DBH up to 42 cm; Figures 4a and 5a). Sap flow on a sapwood area basis (Qs) exhibited less variability than total tree sap flow and was consistently higher in subalpine fir than in whitebark pine (Figures 4b and 5b).

There was a strong linear relationship between total daily sap flow and tree size in both species ($p< 0.001$; Figure 6). The slope of this relationship was significantly different ($p=0.054$ for the interaction DBH*species) indicating that increases in tree size resulted in larger daily accumulated sapflow in subalpine fir compared to whitebark pine. Accumulated daily sap flow on a leaf area basis was significantly greater in whitebark pine than in subalpine fir ($p< 0.001$; Figure 7), while daily sap flow on a sapwood area basis was significantly greater (but to a lesser degree) in subalpine fir ($p < 0.01$; Figure 8). Tree size did not affect sap flow per unit leaf or sapwood area with the exception of whitebark pine where sap flow on a leaf area basis tended to decrease in larger trees ($p=0.08$; Figures 7 and 8).

Stand water use during succession

Total basal area of mixed stands of subalpine fir and whitebark pine in the Bob Marshal Wilderness Complex (BMWC) increased with stand age up to 36 m^2 m^{-2} with a tendency to decrease in the older stand (Figure 9). The contribution of subalpine fir to the total stand basal area increased almost linearly with stand age and was lower than that of whitebark pine at all stand ages. In contrast, basal area of whitebark pine reached a

maximum in stands of ca. 200 years and decreased in the older stand (460 years old). Increases in total stand sapwood basal area (Figure 10a) resulted largely from increases of whitebark pine sapwood. Sapwood basal area of subalpine fir in stands ≥200 years was much lower than that of whitebark pine and remained constant as stands aged. Because subalpine fir allocates a much greater proportion of biomass to foliage compared to whitebark pine (Callaway et al. submitted), total leaf area index of subalpine fir was similar to that of whitebark pine (Figure 10b). Total stand leaf area index increased with age and reached a maximum of 6.3 m^2 m^{-2} in older stands. Stand water use increased asymptotically with stand age up to 1.5 mm day^{-1} with equal contributions by subalpine fir and whitebark pine. Therefore, stand water use in the natural mixed stand was twice that of a stand composed only of whitebark pine. Water use by whitebark pine tended to reach steady state at 200-250 years, while that of subalpine fir increased almost linearly (Figure 10c).

To examine the effects of complete successional replacement of whitebark pine by subalpine fir, an hypothetical situation was simulated in which all trees in the older stand sampled at the BMWC were assumed to be whitebark pine (no succesional replacement) or subalpine fir (complete species replacement). Pure subalpine fir stands had 32% less sapwood basal area than whitebark pine stands, 146% increase in LAI and 22% increase in stand water use.

Discussion

In the subalpine forests of the northwest interior, successional replacement of whitebark pine by subalpine fir may result in substantial increases in stand water use.

This is mainly due to the incursion of subalpine fir into whitebark pine stands in the absence of fire (Keane et al. 1994), and to a lesser degree to higher water use of subalpine firs relative to whitebark pine of the same size. Changes in stand-level water use during succession depend on the overall changes in stand structure (basal area, tree density, LAI ,etc.) and on potential differences in water use between the species being replaced. We will first analyze species-specific differences in physiology and water use and then discuss the implications of these on stand water use during succession as stand structure and species composition change.

Consistent with physiological trends during succession (Bazzaz 1979; Kimings 1987), early successional whitebark pine exhibits higher photosynthesis rates and high PPFD saturation intensity than late successional subalpine fir (Figures 1 and 2). The fact that the two species have similar leaf nitrogen content (Table 1) suggests that photosynthetic nitrogen use efficiency might be greater in whitebark pine compared to subalpine fir. However, Piñol and Sala (submitted), found significantly greater nitrogen content in whitebark pine than in subalpine fir indicating that, at least in some environments, photosynthetic capacity might be greater in whitebark pine (Reich et al. 1997). High photosynthesis rates in whitebark pine might be required to compensate for substantial respiratory costs associated with high allocation to sapwood relative to leaf area in this species (Callaway et al. submitted). Such compensatory responses have been documented within a single species. For instance, Carey et al. (1998) found that respiratory costs associated with increases in relative allocation to sapwood in desert ponderosa pines were compensated for by increases in photosynthesis rates.

Early in the season, under high soil water availability instantaneous water use efficiency of subalpine fir tended to be greater than in whitebark pine. This is because high photosynthetic rates in whitebark pine were also accompanied by high rates of leaf-level water loss (Figures 1 and 7). Stable carbon isotope ratios, however, indicated that in the long term whitebark pine exhibits higher water use efficiency than subalpine fir (Table 1, Piñol and Sala, submitted). It appears then, that whitebark pine increases substantially its water use efficiency later in the season when drought increases. The efficient use of water during drought may enable this early successional species to colonize dry, exposed sites made available by periodical fires (Keane et al. 1994).

Sapflow techniques are now widely used to estimate tree and stand water use (e.g. Čermák et al. 1995; Granier and Loustau, 1994; Granier 1987; Arneth et al. 1996; Cienciala et al. 1994) and a number of studies have shown a good correspondence between the stand level water use estimated from sap flow measurements and that measured using water balance approaches (Granier 1987) or micrometeorological techniques (Granier et al. 1990; Saugier et al. 1997; Arneth et al. 1996). Our results of tree water use are within the range of those reported in the literature for other conifer species (Granier 1987; Čermák et al. 1995; Schiller and Cohen 1995).

While whitebark pine allocates a greater proportion of biomass to sapwood (Callaway et al. submitted), greater reductions in sapflow velocity with sapwood depth were found in the sapwood of whitebark pine (Figure 3). Decreases in sap velocity with sapwood depth is typical of other conifer species (Čermák et al. 1992; Schiller and Cohen 1995) and is related to higher proportion of aspirated pits in the tracheids of older sapwood (i.e. higher proportion of non conducting sapwood) (Mark and Crews 1973).

Thus it appears a larger fraction of the sapwood of whitebark pine is non conducting. This sapwood of lower conductivity (which continues to be respiratory burden) might serve as a storage for water later in the growing season when soil water deficits are likely to develop (Waring and Running 1978, Waring et al. 1979). The tendency of whitebark pine to decrease leaf area-based sap flow rates as trees increase in size (Figure 7) indicates that the efficiency of the hydraulic system to deliver water to leaves decreases as trees increase in age. This is consistent with the hypothesis that productivity in older trees is constrained by hydraulic limitations (Ryan and Yoder 1997). It is important to note, however, that such limitations are apparent in the early successional whitebark pine but not in the late successional subalpine fir, where biomass allocation to leaves is much greater. The combined effect of high sapwood to leaf area ratios and the lower conducting ability of the inner sapwood in whitebark pine results in significantly lower sapwood-related sap flow in whitebark pine compared to subalpine fir (Figures 4, 5 and 8). On a leaf area basis, however, whitebark pine exhibits much higher water loss than subalpine fir (Figure 7). This is because whitebark pine has a much lower leaf to sapwood area ratio than subalpine fir and because whitebark pine canopies are typically open, thus enhancing radiation penetration within the canopy and increasing evaporation at the leaf level. Cienciala et al. (1998) showed that leaf area-based canopy conductance was higher in Pinus sylvestris compared to Picea abies. While pines exhibit high stomatal control of transpiration (relative to the boundary layer) (Loustau et al. 1996), denser canopies and greater needle compaction in subalpine fir may create greater branch and canopy boundary layers (relative to pines), thus imposing some limitation to leaf-level water use. High relative allocation to foliage in subalpine fir offsets leaf level reductions in water

loss and cumulative daily sap flow of subalpine fir is similar (in smaller trees) or even greater (in larger trees) than that of whitebark pine (Figure 6).

In contrast to others reports (Schiller and Cohen 1995), we found a strong correlation between total cummulative sap flow and tree size in both species (Granier et al. 1990). This highly significant relationship allowed us to estimate stand water use in natural stands in the BMWC, where fire suppression policies during the past 60 -80 years have allowed the gradual incursion of subalpine fir into whitebark pine stands (Keane et al. 1994). Such extrapolation assumes that the relationship between tree size and water use in the BMWC is the same as in our sampling site and that it remains constant as stands age. We do not expect large site changes in this relationship because our sampling site and the 12 stands selected from the BMWC belong to the same habitat type (Pfister et al. 1977). This habitat type classification is based on climatic variables and on vegetation characteristics of the overstory and understory. The inclusion of the understory is particularly relevant because it reflects prevailing soil water resources. Further, tree density and basal area in our sampling site were similar to those in the BMWC stands. The degree to which the tree size-water use relationship remains constant as stands age and LAI increases needs to be tested. However, as stands age and LAI increases it is expected that the early successional, shade intolerant whitebark pine would experience proportionally greater reductions in water loss. This would magnify our results at the tree level and corroborate our prediction at the stand level that the incursion of subalpine fir into pure whitebark pine stands may result in large increases in stand water use (Figure 10). It is important to emphasize that our models of tree water use were developed early in the season under conditions of high water availability (shortly after snowmelt) and of

relatively high evaporative demand. Therefore our estimates of stand water use are maximum values expected under similar conditions. The extent to which water resources are consumed early in the season, will greatly influence water availability late in the season, particularly during dry summers.

Historically, fire frequency in the subalpine forests of the interior northwest ranged between 50 and 300 years (Arno 1980). These fires killed fire sensitive subalpine fir and maintained open whitebark pines stands (Arno 1986; Arno and Hoff 1989). In the absence of fire, the incursion of subalpine fir results in gradual increases in stand density. Regeneration of the shade intolerant whitebark pine might become increasingly limited and eventually whitebark pine will be replaced. While a large fraction of the increased water use in older, fire-excluded stands results from the incursion of subalpine fir and associated increase in LAI, a smaller but significant fraction results from species-specific differences in water use. For instance, comparisons of water use in hypothetical old pure subalpine fir stands vs. pure whitebark pine stands (assuming the same size distribution as in natural mixed stands) indicates that water use in pure subalpine fir stands is 22% greater than in pure whitebark pine stands (Table 2). Although this analysis ignores differences in size distributions between whitebark pine and sabalpine fir stands it indicates that species-specific differences in water relations might influence stand-level water use during succession.

Stand-level increases in water use associated with successional species replacement may have important ecological consequences. At the stand level, decreases in soil water resources may increase physiological stress and susceptibility to pathogens, which could ultimately decrease productivity. At the

watershed level, water resources downstream may decrease with consequent effects on lowland vegetation and wildlife.

Acknowledgements

This research was supported by the USDA Forest Service, Rocky Mountain Research Station, INT-95086-RJVA to R. Callaway and A. Sala and USDA NRIGCP 95-37101-1683 to R. Callaway. We are very thankful to Erick Aschehough, Andrew Carroll, Trevor Laboski, Kevin Murray and Jodee Smith for enduring long days in the field. Jodee Smith and Willow Foster spent long hours in the lab working on sap flow data.

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Table 1. Carbon isotope ratios and total leaf nitrogen content of mature needles of whitebark pine and subalpine fire. Values are the average of 20 trees per species (± standard error). Different letters indicate statistically significant differences between species ($p<0.05$).

	$\delta^{13}C$, ‰	%N
Whitebark Pine	-25.55 ± 0.22[a]	1.08 ± 0.03[a]
Subalpine Fir	-26.20 ± 0.19[b]	1.11 ± 0.03[a]

Table 2. Estimated sapwood basal area, LAI and stand-level water use in a hypothetical situation in which all trees in the 458 year old stand sampled at the BMWC were assumed to be whitebark pine (no successional replacement) or subalpine fir (complete species replacement). Total basal area (whitebark pine and subalpine fir combined) was 31.9 m^2 ha^{-1}. % change is relative to whitebark pine.

	Sapwood m^2 ha^{-1}	LAI m^2 m^{-2}	Water Use Kg m^{-2} day^{-1}
Whitebark Pine	5.36	3.78	1.35
Subalpine Fir	3.63	9.31	1.65
% Change	- 32.5	+ 146.4	+ 22.1

Figure Captions

Figure 1. Diurnal courses of photosynthesis rates (A), transpiration rates (E) and instantaneous water use efficiency (WUE) of mature exposed needles of whitebark pine and subalpine fir. Data are the average of four trees (± SE).

Figure 2. Response of the photosynthetic rates in whitebark pine and subalpine fir to photosynthetic photon flux density. Data are the average of four different trees. The curve was fit as 2^{nd} order polynomial to illustrate tendencies.

Figure 3. Changes in sap velocity (relative to the maximum) with sapwood depth (thermocouple locations 1 to 3, from closest to the cambium to closest to the heartwood) in whitebark pine and subalpine fir. Thermocouple distances from the cambium varied according to probe length. However, because probes of increasing length were installed in trees of increasing size, locations 1, 2 and 3 represent equivalent distances relative to total sapwood depth. Both, whitebark pine and subalpine fir received the same proportion of 20, 25 30 and 35 mm long probes.

Figure 4. Changes in sap flow per tree (Q, panel A) and sapwood-related sapflow (Qs, panel B) in whitebark pine and subalpine fir, and leaf to air vapor pressure difference (LAVPD, mole fraction, panel C) during July 12, 96. Values are the average of 8 subalpine firs and 6 whitebark pines. Bars are standard errors.

Figure 5. Changes in sap flow per tree (Q, panel A) and sapwood-related sapflow (Qs, panel B) in whitebark pine and subalpine fir, and leaf to air vapor pressure difference (LAVPD, mole fraction, panel C) during July 14, 96. Values are the average of 8 subalpine firs and 9 whitebark pines. Bars are standard errors.

Figure 6. Relationship between daily sapflow per tree (Q, from 5 a.m. to 10:30 p.m.) and DBH. Best fits were obtained with square root transformations of Q. Regression lines are SQRT(Q) = 0.421 + 0.179 DBH, r^2= 0.97, p<0.0001 for subalpine fir and SQRT(Q) = 0.565 + 0.152 DBH, r^2= 0.94, p<0.001 in whitebark pine. There was a significant DBH (p<0.0001) and DBH*species interaction (p= 0.054) indicating that the slopes of the two lines are significantly different.

Figure 7. Relationship between leaf area related daily sapflow (Q_L, from 5 a.m. to 10:30 p.m.) and DBH. Regression lines are Q_L = 0.247 - 0.001 DBH, r^2= 0.09, p = 0.48 for subalpine fir and Q_L = 0.523 - 0.005 DBH, r^2= 0.34, p = 0.08 in whitebark pine. There was a significant species effect (p<0.0001).

Figure 8. Relationship between sapwood area related daily sapflow (Q_S, from 5 a.m. to 10:30 p.m.) and DBH. Regression lines were not significant for either of the two species. There was, however, a significant species effect (P< 0.01).

Figure 9. Basal area of subalpine fir, whitebark pine and the total for the stand in 12 natural stands of varying age in the Bob Marshall Wilderness Complex, Montana. The curve was fit as 2nd order polynomial to illustrate tendencies.

Figure 10. Sapwood basal area (panel A), leaf area index (panel B) and estimated daily stand water use on a ground area basis (panel C) of subalpine fir, whitebark pine and the total for the stand in 12 natural stands of varying age in the Bob Marshall Wilderness Complex, Montana. Curves were fit as 2nd order polynomials to illustrate tendencies.

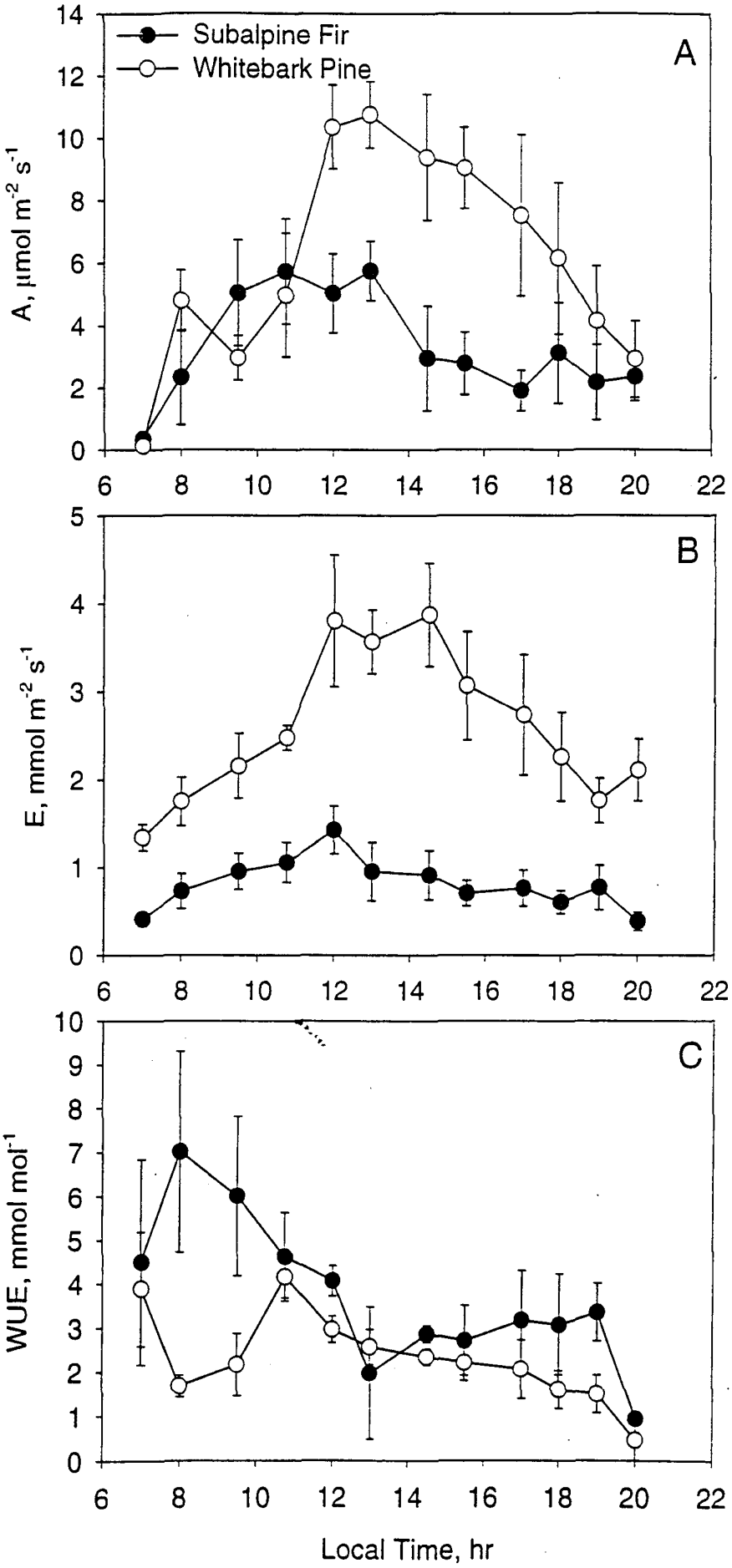
Subalpine Fir
Whitebark Pine
A
B
C
A, µmol m-2 s-1
E, mmol m-2 s-1
WUE, mmol mol-1
Local Time, hr

Fig. 1

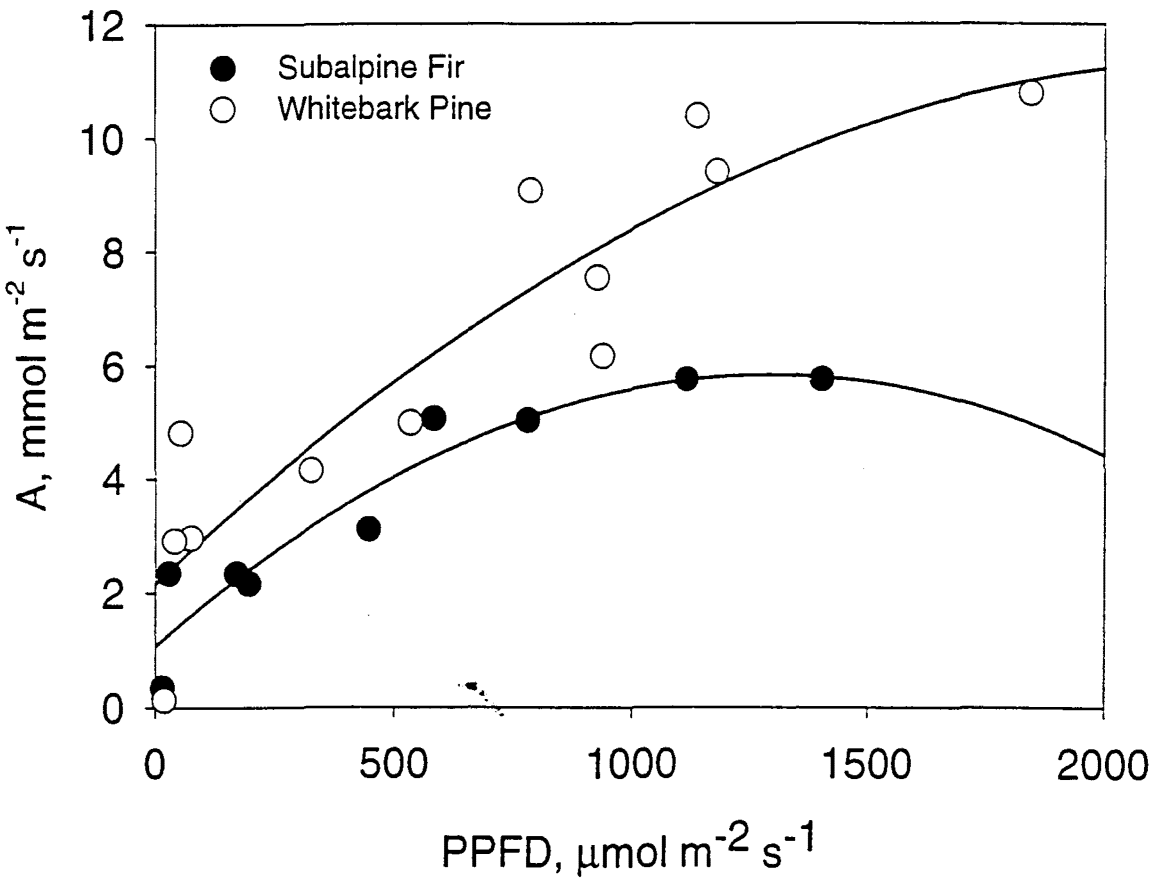
Subalpine Fir
Whitebark Pine
A, mmol m-2 s-1
PPFD, µmol m-2 s-1
0
2
4
6
8
10
12
0
500
1000
1500
2000

Fig. 2

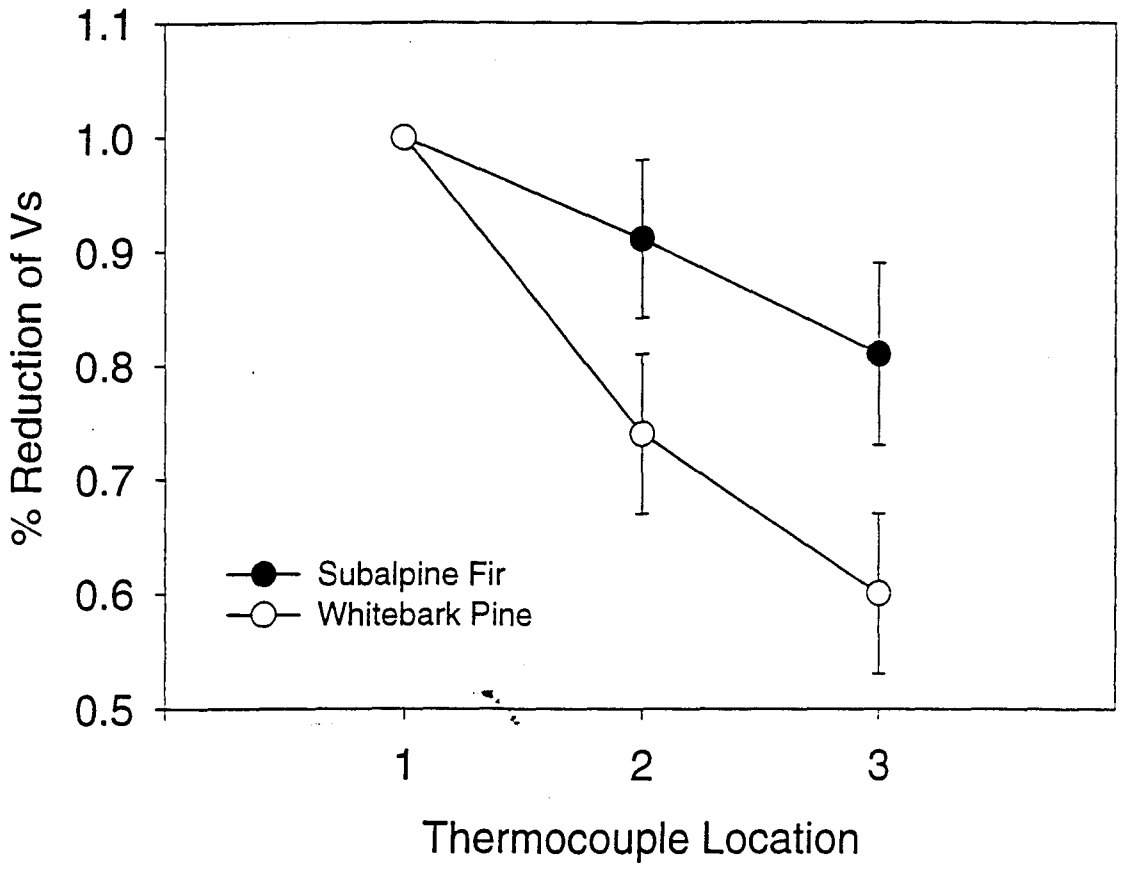
1.1
1.0
0.9
0.8
0.7
0.6
0.5
% Reduction of Vs
Subalpine Fir
Whitebark Pine
1
2
3
Thermocouple Location

Fig. 3

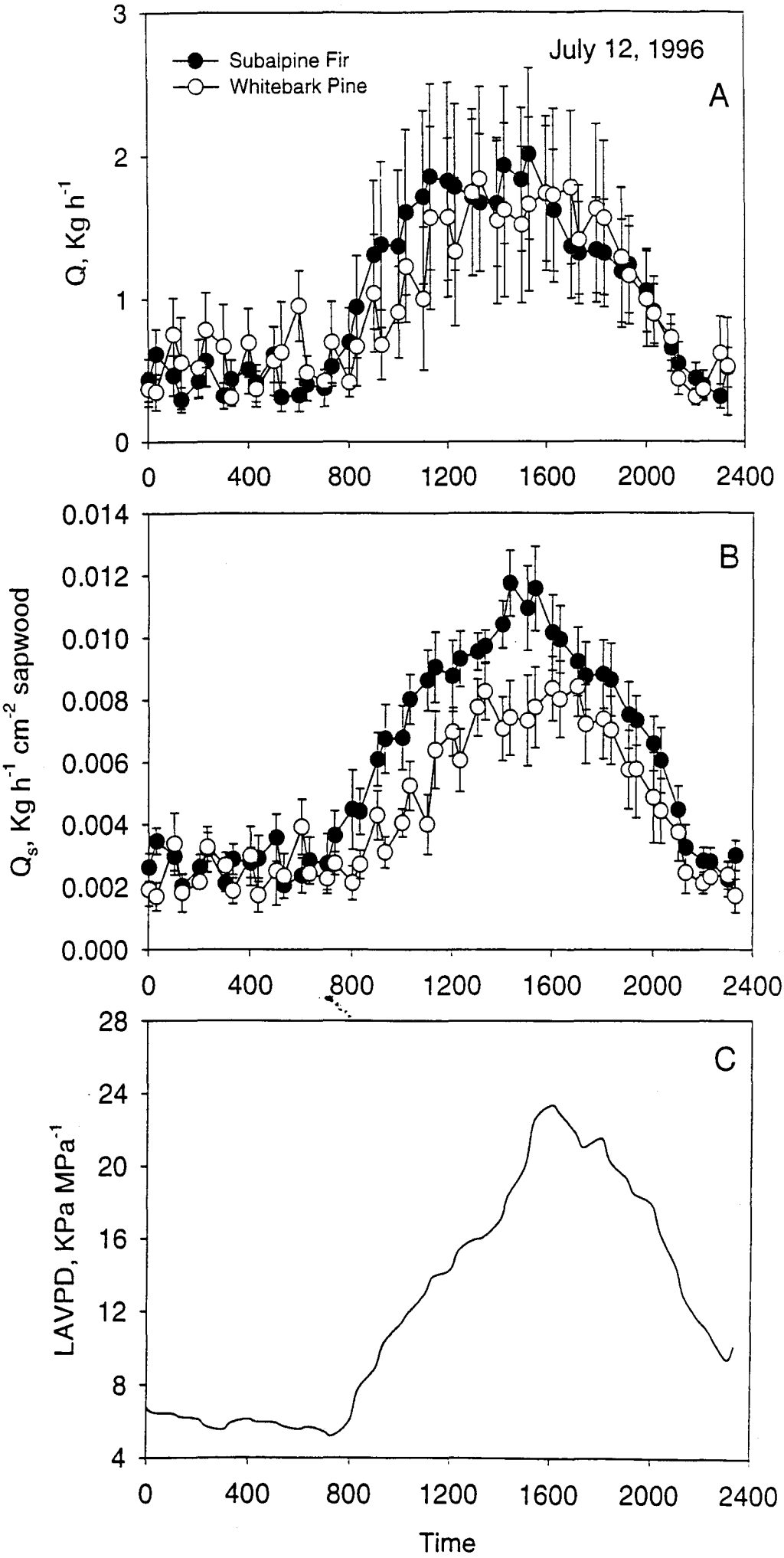
Subalpine Fir
Whitebark Pine
July 12, 1996
A
B
C
Q, Kg h-1
Qs, Kg h-1 cm-2 sapwood
LAVPD, KPa MPa-1
Time
0
400
800
1200
1600
2000
2400
0.000
0.002
0.004
0.006
0.008
0.010
0.012
0.014
4
8
12
16
20
24
28

Fig. 4

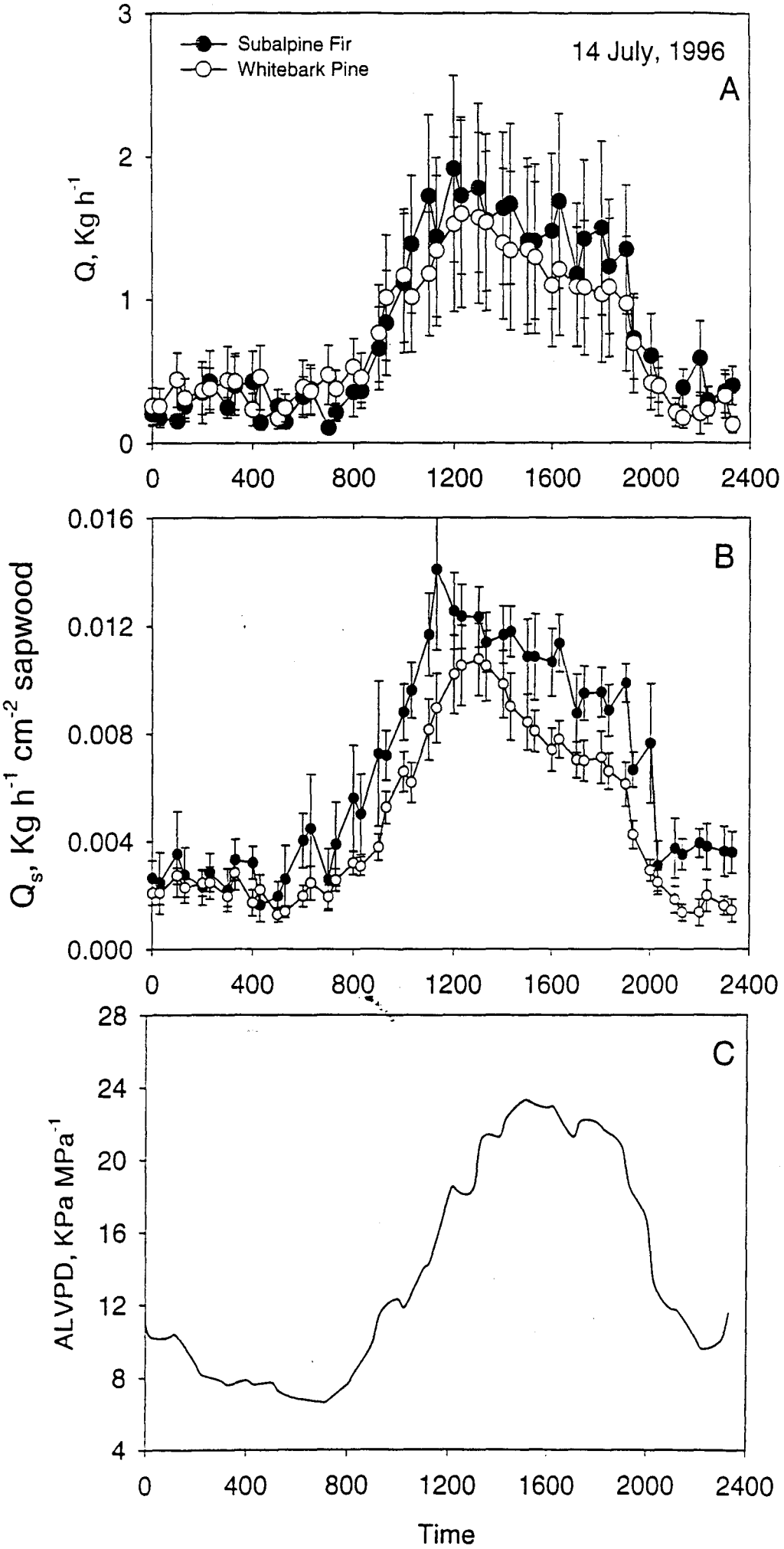
Subalpine Fir
Whitebark Pine
14 July, 1996
A
B
C
Q, Kg h-1
Qs, Kg h-1 cm-2 sapwood
ALVPD, KPa MPa-1
Time
0
400
800
1200
1600
2000
2400
0.000
0.004
0.008
0.012
0.016
4
8
12
16
20
24
28

Fig. 5

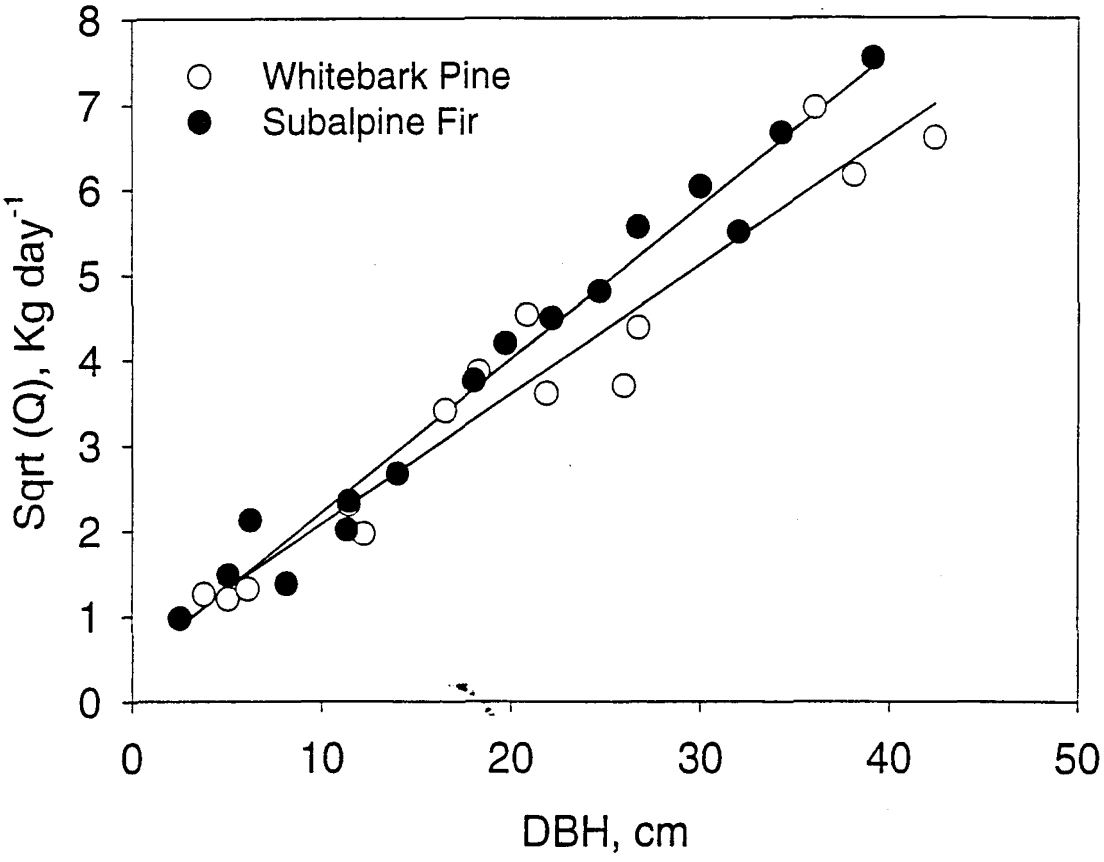
Whitebark Pine
Subalpine Fir
Sqrt (Q), Kg day-1
DBH, cm
0
1
2
3
4
5
6
7
8
0
10
20
30
40
50

Fig. 6

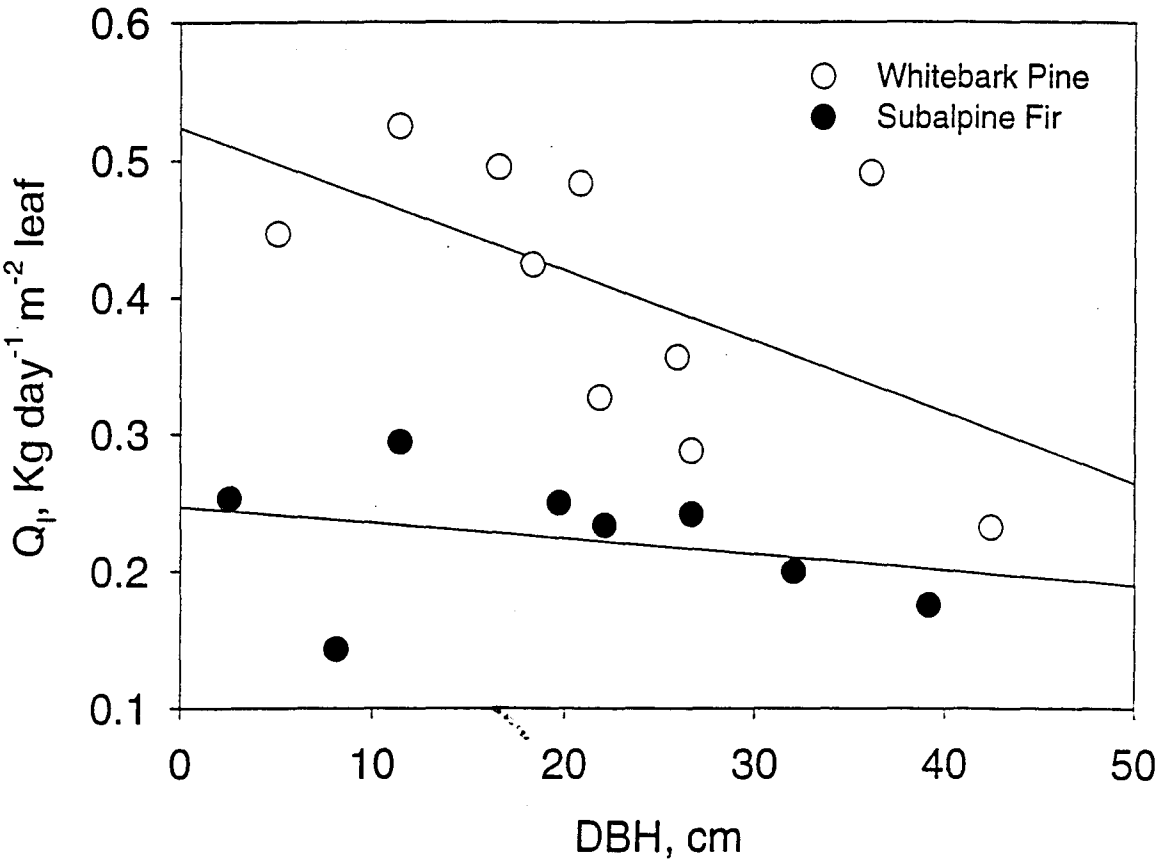
0.6
0.5
0.4
0.3
0.2
0.1
0
10
20
30
40
50
Whitebark Pine
Subalpine Fir
Q_l, Kg day^{-1} m^{-2} leaf
DBH, cm

Fig.7

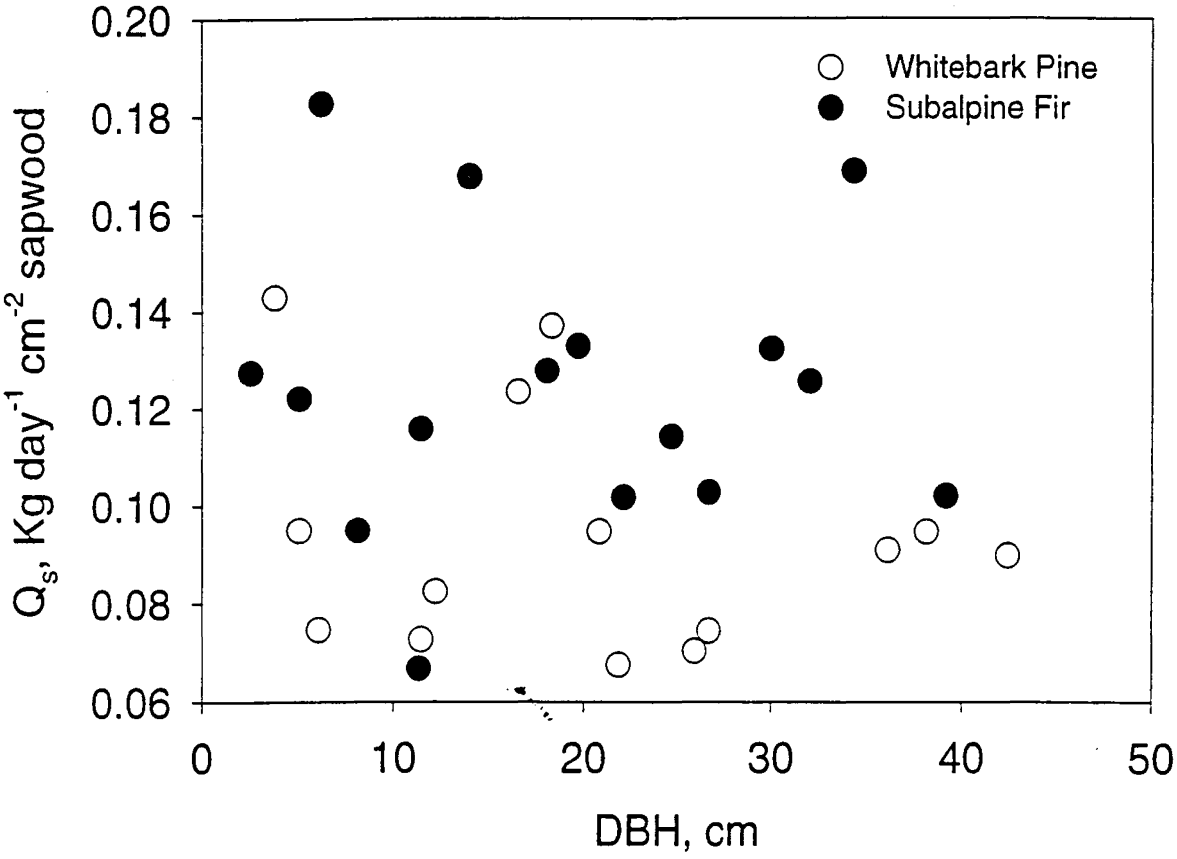
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
Q_s, Kg day^{-1} cm^{-2} sapwood
0
10
20
30
40
50
DBH, cm
Whitebark Pine
Subalpine Fir

Fig. 8

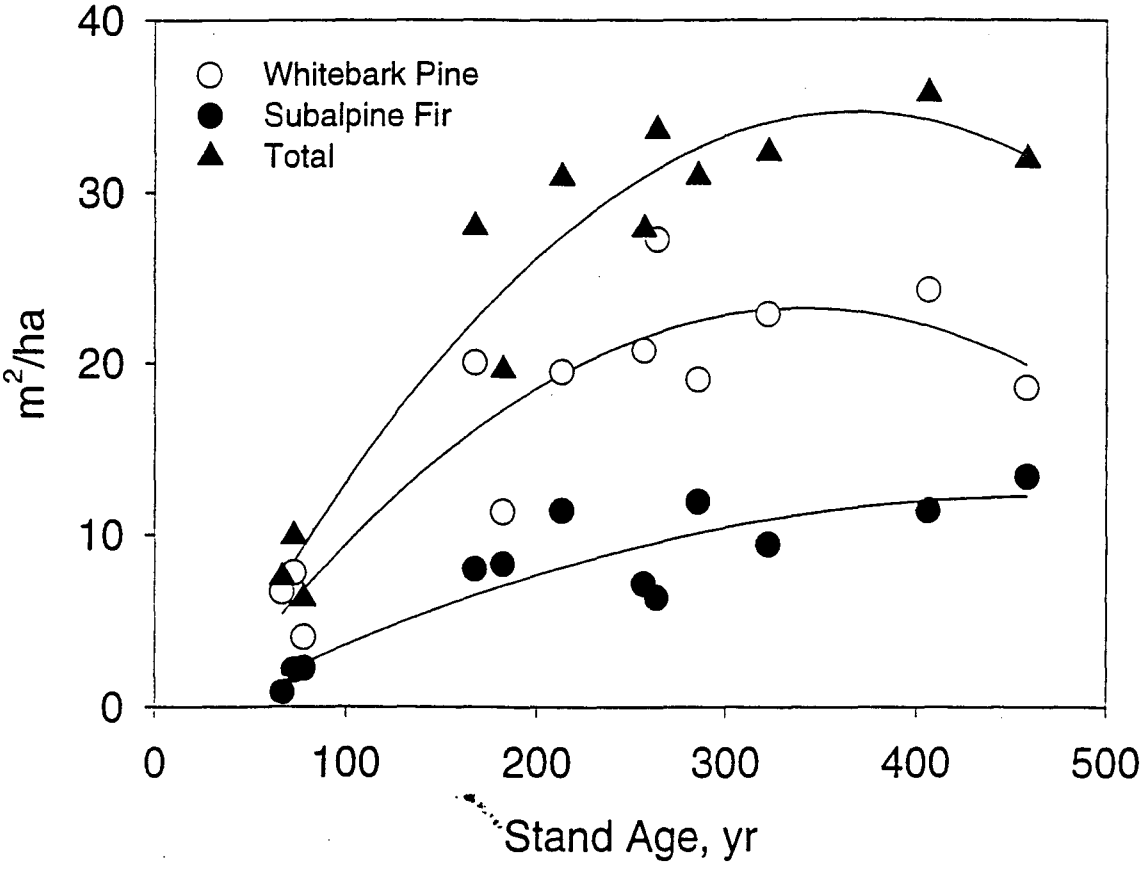
40
30
20
10
0
0
100
200
300
400
500
m²/ha
Stand Age, yr
Whitebark Pine
Subalpine Fir
Total

Fig. 9

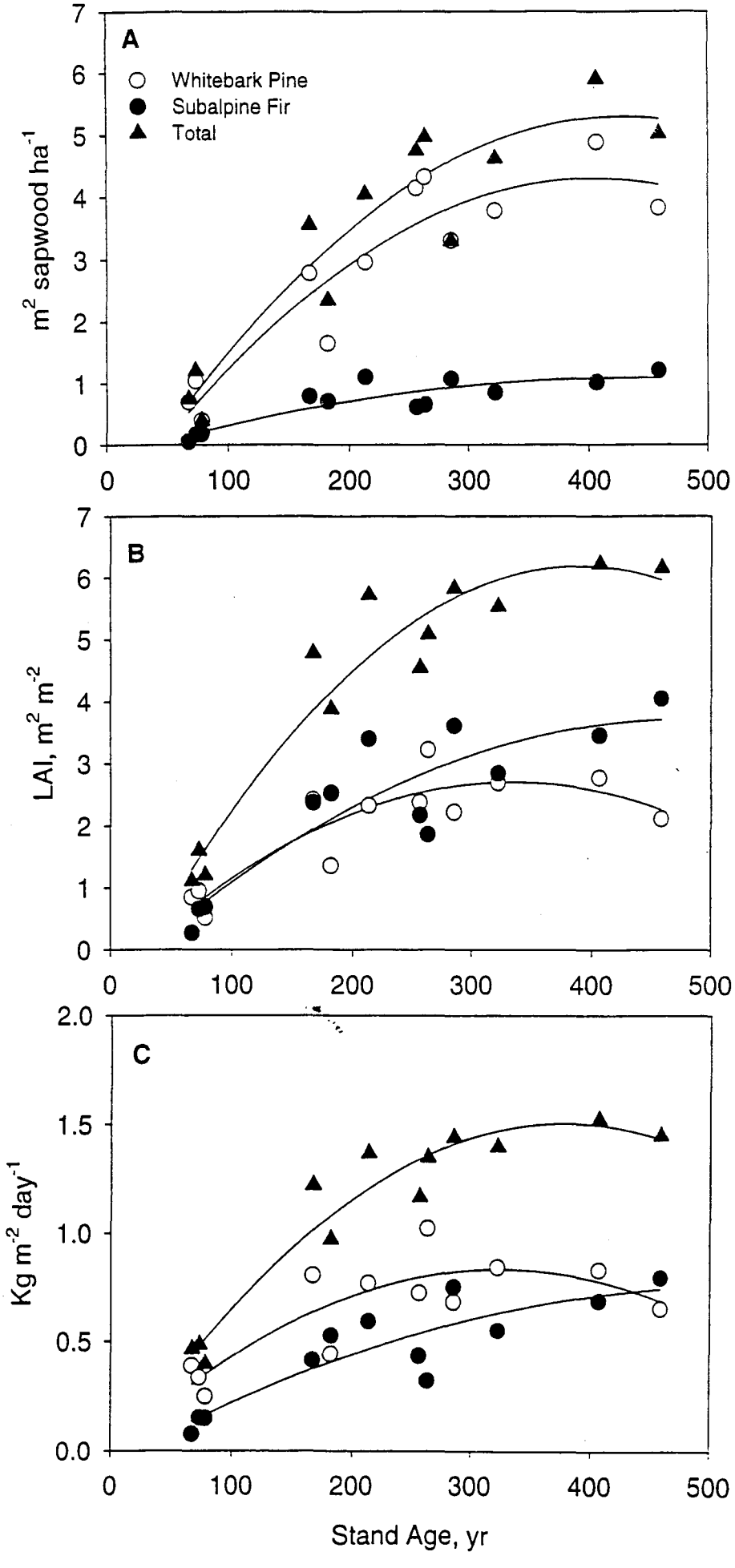
A
Whitebark Pine
Subalpine Fir
Total
m2 sapwood ha-1
B
LAI, m2 m-2
C
Kg m-2 day-1
Stand Age, yr

Fig. 10